

507.67

ANNALS OF THE
SOUTH AFRICAN MUSEUM

VOLUME 85

ANNALE VAN DIE
SUID-AFRIKAANSE MUSEUM

BAND 85



ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 85 BAND



THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

DIE TRUSTEES VAN DIE
SUID-AFRIKAANSE MUSEUM
KAAPSTAD

1981-1982

SET, PRINTED AND BOUND IN THE REPUBLIC OF SOUTH AFRICA BY
THE RUSTICA PRESS (PTY.) LTD., WYNBERG, CAPE

C914

LIST OF CONTENTS

	<i>Page</i>
AVERY, D. M. Micromammals as palaeoenvironmental indicators and an interpretation of the Late Quaternary in the southern Cape Province, South Africa. (Published January 1982.)	183
DINGLE, R. V. The Campanian and Maastrichtian Ostracoda of south-east Africa. (Published October 1981.)	1

NEW GENERIC NAMES PROPOSED IN THIS VOLUME

	<i>Page</i>
<i>Dutoitella</i> Dingle, 1981	84
<i>Klingerella</i> Dingle, 1981	57
<i>Ponticulocythere</i> Dingle, 1981	76

ANNALS

OF THE SOUTH AFRICAN
MUSEUM



CAPE TOWN

INSTRUCTIONS TO AUTHORS

1. **MATERIAL** should be original and not published elsewhere, in whole or in part.

2. **LAYOUT** should be as follows:

- (a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
Author's(s') name(s)
Address(es) of author(s) (institution where work was carried out)
Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
- (c) *Table of contents* giving hierarchy of headings and subheadings
- (d) *Introduction*
- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
- (f) *Summary*, if paper is lengthy
- (g) *Acknowledgements*
- (h) *References*
- (i) *Abbreviations*, where these are numerous

3. **MANUSCRIPT**, to be submitted in triplicate, should be typewritten and neat, double spaced with 2.5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. **ILLUSTRATIONS** should be reducible to a size not exceeding 12 × 18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35 × 47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

5. **REFERENCES** cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid.*, *idem*, *loc. cit.*, *op. cit.* are not acceptable):

(a) Author's name and year of publication given in text, e.g.:

- 'Smith (1969) describes ...'
- 'Smith (1969: 36, fig. 16) describes ...'
- 'As described (Smith 1969a, 1969b; Jones 1971)'
- 'As described (Haughton & Broom 1927) ...'
- 'As described (Haughton *et al.* 1927) ...'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969a, 1969b) and not Smith (1969, 1969a).

For books give title in italics, edition, volume number, place of publication, publisher.

For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

Examples (note capitalization and punctuation)

- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris **88**: 100-140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* **4**: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **85** Band
October **1981** Oktober
Part **1** Deel



THE CAMPANIAN AND MAASTRICHTIAN
OSTRACODA OF SOUTH-EAST AFRICA

By

R. V. DINGLE

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33, 45(1)

EDITOR/REDAKTRISE

Ione Rudner

Copyright enquiries to the South African Museum

Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 86813 019 2

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

THE CAMPANIAN AND MAASTRICHTIAN OSTRACODA OF SOUTH-EAST AFRICA

By

R. V. DINGLE

Department of Geology, University of Cape Town

(With 81 figures and 20 tables)

[MS. accepted 6 November 1980]

ABSTRACT

78 species, representing 46 genera of ostracoda are recorded from the Campanian and Maastrichtian strata of south-east Africa, where rocks of this age have been sampled in the Natal-Zululand Basin, on the Transkei Swell, and in the Outeniqua Basin (on the Agulhas Bank). 35 of the species are new, 34 have previously been described from south-east Africa, 1 previously described from Australia, and 8 are left in open nomenclature. 1 new subfamily (Unicapellinae), and 3 new genera (*Klingerella*, *Ponticulocythere*, and *Dutoitella*) are erected. Of the 35 new species, the following 23 are formally described: *Cytherelloidea mfoloziensis*, *Platella africana*, *Pontocyprella nibelaensis*, *Pariceratina hirsuta*, *Eucytherura?* *pyramidatus*, *Cytheropteron brenneri*, *Pedicythere fragilis*, *Apateloschizocythere mclachlani*, *Amphicytherura armatus*, *Klingerella aranearius*, *Krithe nibelaensis*, *Pondoina igodaensis*, *Xestoleberis luciaensis*, *Ponticulocythere biremis*, *Dutoitella dutoiti*, *D. mimica*, *Haughtonileberis nibelaensis*, *Oertliella maastrichtia*, *Hermanites?* *arcus*, *Parvacythereis monziensis*, *Curfsina monziensis*, *Cativella?* *dubia*, and *Australileberis stangerensis*.

Population analyses on the faunas from Zululand lead to the recognition of six distinctive ostracod assemblages, that in turn can be related to various palaeosedimentary environments. All were considered to have been low-energy, open-water, normal marine situations. Further consideration of these data, including the use of a Cytheracea-Cytherellidae-Bairdiacea/Cypridacea triangular diagram (CCBC plot), allows a reconstruction of the Campanian-Maastrichtian palaeogeography of Zululand, and the recognition of local late Cretaceous sea-level fluctuations. A comparison with other Gondwanide localities reveals a relatively close relationship at the generic level between south-east Africa and western Australia and east Africa, and only weak links with west Africa and South America. Finally, an ostracod zonal scheme is proposed, based on the Zululand faunas.

CONTENTS

	PAGE
Introduction	2
Regional stratigraphy and sampling localities	3
Systematic descriptions	12
Discussion	131
Palaeoecology	132
Northern area	132
BH-9 borehole and Zululand outcrops	132
JC-1 borehole	146
Campanian-Maastrichtian palaeogeography of southern Natal-Zululand Basin	149
Eastern area	152
Igoda	153
Needs Camp	154
Umzamba	156

Southern area: Agulhas Bank	156
Summary	159
Biostratigraphy	160
South-east Africa	160
Phylogeny—species distribution (appearances)	160
Ostracod zonal scheme	163
Phylogeny—higher taxa	166
Phylogeny—species distribution (extinctions)	170
Comparison with other Gondwanide localities	170
Western Australia	172
East Africa	174
West Africa	174
South America	175

INTRODUCTION

The purpose of this contribution is to document and discuss as fully as possible the taxonomy, palaeoecology and stratigraphic distribution of the Campanian and Maastrichtian ostracod faunas of south-east Africa.

Marine sediments of this age in south-east Africa occur in two large continental margin basins (Outeniqua and Natal–Zululand) which are separated by the generally positive Transkei Swell region on which rest small, thin patches of marine Mesozoic strata (Dingle 1978) (Fig. 1). The St Johns Basin on the narrow continental shelf off the Transkei coast may contain uppermost Cretaceous sediments. Campanian–Maastrichtian times were marked by relatively high sea-levels as the Upper Cretaceous marine transgression reached its peak, with the result that whilst the basinal facies are merely the youngest strata in a thick Mesozoic pile, the thin deposits over the Transkei Swell rest directly on pre-Mesozoic basement (Figs 1, 3).

The first studies on Campanian–Maastrichtian marine ostracods from south-east Africa were made by Chapman (1916) when he described the microfauna of the late Campanian/early Maastrichtian limestones from the 'Lower' quarry at Needs Camp. (There is no evidence to indicate that in his 1904 or 1923 papers Chapman sampled horizons as high as Campanian at the Umzamba cliff sections in Transkei.) Chapman (1916) recorded three species of ostracod from Needs Camp, and since then the only other descriptions of ostracods of this age from south-east Africa were by Dingle (1971, 1980) on Maastrichtian from the Outeniqua Basin, and Santonian–Campanian from the Richards Bay BH–9 borehole, Zululand, respectively.

The present study, together with a reassessment of the earlier work, has resulted in the recognition of 78 species of ostracods in the Campanian and Maastrichtian sediments of south-east Africa (Table 1). These have been allocated to 46 genera, with 8 types in open nomenclature. In the Natal–Zululand Basin, where ostracods are abundant, the faunas can be grouped into 4 distinct assemblages, 2 of which can be further subdivided. This allows the recognition of 6 palaeosedimentary environments which are shown to have alternated during Campanian–Maastrichtian time. Sparser faunas from the other areas are com-

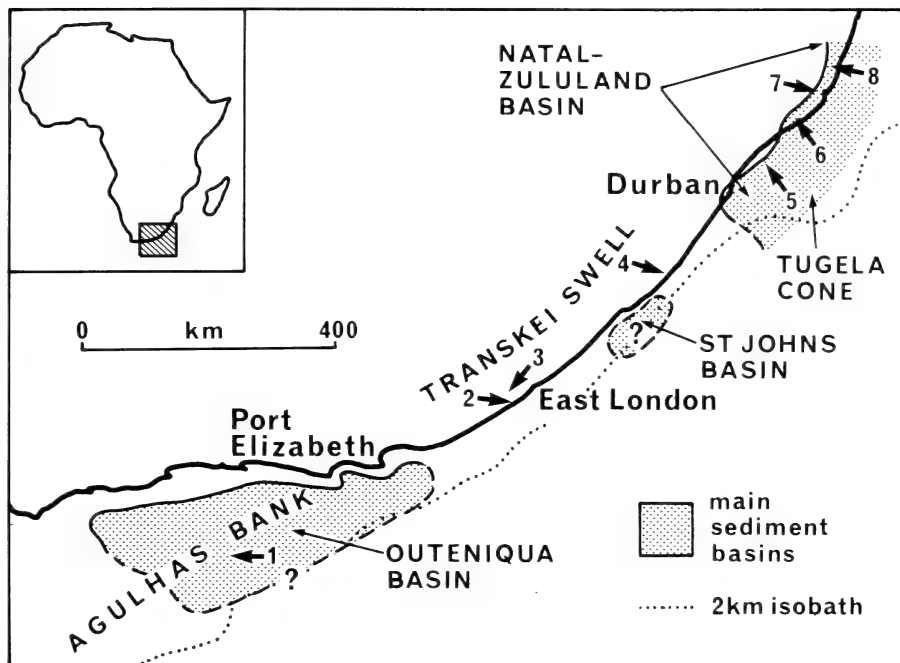


Fig. 1. Distribution of Campanian-Maastrichtian sediments in south-east Africa (shaded). Numbers refer to sampling localities: 1—sample 818, Agulhas Bank; 2—Igoda estuary; 3—Lower or East Quarry, Needs Camp; 4—Umzamba Cliff; 5—JC-1 borehole; 6—BH-9 borehole, Richards Bay; 7—Monzi and Mfolozi River outcrops (Kennedy & Klinger 1975 localities 20 & 21); 8—Nibela Peninsula (Kennedy & Klinger 1975 localities 110 & 113).

pared with the better-known ostracod assemblages from Natal-Zululand, and suggestions for their palaeoenvironments are advanced.

The temporal distribution of the various ostracod species in Zululand, Richards Bay BH-9 borehole, and the Agulhas Bank is shown in Table 2 and is related to the ammonite zonation of Kennedy & Klinger (1975). A consideration of the age ranges of some of the diagnostic, and less environmentally-bound species, leads to a proposed ostracod zonation scheme for the Zululand Campanian-Maastrichtian succession. 4 zones and 6 subzones (a total of 8 separate periods) are recognized.

REGIONAL STRATIGRAPHY AND SAMPLING LOCALITIES

Figures 1-2 show the approximate extent of the Campanian and Maastrichtian sediments in south-east Africa and the localities from which samples were available for study. Measured sections and sampled horizons are shown in Figure 3, and where they coincide with localities examined by Kennedy & Klinger (1975), the original notation system has been retained to allow correla-

TABLE 1
Geographical distribution of ostracods in Campanian and Maastrichtian strata of south-east Africa

	Zulu- land	BH-9	JC-1	Um- zamba	Igoda	Needs Camp	Agulhas Bank
<i>Cytherella</i> sp.	×	×	×		×		×
<i>Cytherelloidea contorta</i>	×	×					
<i>C. umzambaensis</i>	×	×					
<i>C. griesbachi</i>		×					
<i>C. mfoloziensis</i>	×						
<i>Platella africana</i>	×						×
<i>Bairdoppilata andersoni</i>	×	×		?×	×	×	×
<i>B. andersoni aequalis</i>						×	
<i>B. africana</i>						×	
<i>B. cf. africana</i>			×				
<i>B. sp. A</i>					×		
<i>Bythocypris richardsbayensis</i>	×	×			×		×
<i>B?</i> sp.			×				
<i>Paracypris umzambaensis</i>	×	×			×		
<i>P. zululandensis</i>	×	×					×
<i>P. sp. A</i>					×		
<i>P. sp.</i>			×				
<i>Pontocyprella nibelaensis</i>	×						×
<i>P. sp.</i>						×	
<i>Pariceratina hirsuta</i>	×						
<i>Eucytherura? pyramidatus</i>	×						
<i>Cytheropteron brenneri</i>	×						
<i>C. cf. westaustraliense</i>	×						
<i>Pedicythere fragilis</i>	×						
<i>Apateloschizocythere mclachlani</i>	×						
<i>A. laminata</i>							×
<i>Amphicytherura tumida</i>		×		×			
<i>A. zululandensis</i>		×					
<i>A. armatus</i>	×						
<i>A. sp. A</i>	×						
<i>Klingerella aranearius</i>	×						
<i>Hutsonia? sp.</i>					×		
<i>Krithe nibelaensis</i>	×						×
<i>K. sp. A</i>			×				
<i>Pondoina igodaensis</i>					×		
<i>Xestoleberis luciaensis</i>	×	×			×		
<i>Buntonia? sp.</i>					×		
<i>Brachycythere sicarius</i>	×	×					
<i>B. longicaudata</i>	×	×		×	×		
<i>Pterygocythere lanceolata</i>	×						
<i>Ponticulocythere biremis</i>	×						
<i>Agulhasina quadrata</i>							×
<i>Unicapella sacsi</i>	×	×					×
<i>U. reticulata</i>		×					
<i>Dutoitella dutoiti</i>	×						
<i>D. mimica</i>			×				×
<i>Haughtonileberis haughtoni</i>		×					
<i>H. vanhoepeni</i>	×	×					
<i>H. fissilis</i>	×	×		×			
<i>H. nibelaensis</i>	×	×					
<i>Rayneria nealei</i>		×					

85(1)	Zulu- land	BH-9	JC-1	Um- zamba	Igoda	Needs Camp	Agulhas Bank
<i>Cythereis klingerii</i>	×	×					
<i>C. transkeiensis</i>				×	×		
<i>Oertliella</i> sp. A.		×					
<i>O. pennata</i>		×					
<i>O. africana</i>	×	×					
<i>O. maastrichtia</i>	×						
<i>Gibberleberis elongata</i>		×					
<i>G.</i> sp. A	×						
<i>Trachyleberis minima</i>		×					
<i>T. zululandensis</i>	×	×					
<i>T. schizospinosa</i>							×
<i>Hermanites kennedyi</i>	×	×			×		
<i>H?</i> <i>arcus</i>	×						
<i>H?</i> cf. <i>arcus</i>					×	×	
<i>Parvacytheis monziensis</i>	×						
<i>P. spinosa</i>							×
<i>Curfsina monziensis</i>	×						
<i>Cativella?</i> <i>dubia</i>	×						
<i>Phacorhabdotus?</i> <i>anomala</i>			×				×
<i>P?</i> sp. A			×				
<i>Australileberis stangerensis</i>			×				
<i>Paraplatycosta reticulata</i>							×
Indet. sp. 1	×						
Indet. sp. 2	×						
Indet. sp. 3	×						
Indet. sp. 4	×						
Indet. sp. 5					×		
Indet. sp. 6						×	
Indet. sp. 7			×				
Indet. sp.			×				
Totals	44	28	11	5	15	6	15
78 species, 46 genera							

tion with their ammonite zonation. These workers recognized eight subdivisions in the Campanian–Maastrichtian of Zululand based on ammonite assemblages, and although these were intended to be provisional upon the establishment of a more sophisticated scheme, details of their zonation are given in Table 3 to allow the extension of our ostracod ranges outside the south-east African region.

OUTENIQUA BASIN (locality 1 on Figs 1, 3).

A single sea-floor sample from the Alphard Formation consisting of light olive, clayey sand containing abundant glauconite grains, pyrite and shell fragments, and occasional fish teeth. Position: 35°20,0'S 23°17,0'E from a sea-floor depth of 1 203 m. The rich and well-preserved microfauna of this sample was originally described by Dingle (1971). It contains, amongst others, the following planktonic foraminifera: *Gublerina reniformis* (Marie), *Rugoglobigerina rugosa* (Plummer), *R. rugosa rotundata* Brönnimann, *Globotruncana arca* (Cushman), *G. stuarti* (de Lapparent), and *G. aegyptiaca* Nakkady, which indicate a Middle–Upper Maastrichtian age (Postuma 1971). This is corroborated

stage divisions	locality	bed number	<i>Rayneria nealei</i>	<i>Amphicytherura tumida</i>	<i>Haughtonileberis haughtoni</i>	<i>Oerthella pennata</i>	<i>O. sp. A</i>	<i>Gibberleberis elongata</i>	<i>Cytherelloidea griesbachi</i>	<i>Haughtonileberis vanhoepeni</i>	<i>Cytherelloidea umzambaensis</i>	<i>Haughtonileberis fissilis</i>	<i>Brachythere sicarius</i>	<i>Cythereis klingeri</i>	<i>Paracypris</i> spp	<i>Brachythere longicaudata</i>	<i>Cytherella</i> sp.	<i>Bairdopillata andersoni</i>	<i>Bythocypris richardsbayensis</i>	<i>Trachyleberis minima</i>	<i>Amphicytherura zululandensis</i>	<i>Cytherelloidea contorta</i>	<i>Oerthella africana</i>	<i>Trachyleberis zululandensis</i>	<i>Xestoleberis luciaeensis</i>	<i>Haughtonileberis nibelaensis</i>
MIII	818																×	×	×							
		8														×	×	×	×					×	×	
MII		7/3												×	×	×	×	×	×					×	×	
		7/2													×	×	×	×	×					×	×	
		7/1												×	×	×	×	×	×					×	×	
	20	5												×	×	×	×	×	×					×	×	
		3													×	×	×	×	×					×	×	
MI		1/3									×	×			×	×	×	×	×					×	×	
		1/2													×	×	×	×	×					×	×	
		1/1													×	×	×	×	×			×		×	×	
CV	21	1															×	×							×	
		13												×			×	×	×					×	×	
		11								×				×		×	×	×	×					×	×	
CIV	113	3								×				×		×	×	×	×					×	×	
		1								×				×	×	×	×	×	×					×	×	
		0							×	×				×	×	×	×	×	×					×	×	
		21													×		×	×	×							
CHII		19									×	×		×		×	×	×	×						×	
	110	14							×	×				×	×	×	×	×	×		×	×			×	
		2								×				×		×	×	×	×						×	
		82.0								×		×	×	×	×		×	×	×					×	×	
		87.0								×		×	×	×	×	×	×	×	×					×	×	
CII		88.0			×	×		×	×	×	×	×	×	×	×	×	×	×	×					×	×	
	BH-9	89.0			×							×		×		×	×	×						×	×	
		92.3		×				×		×				×	×	×	×	×	×						×	
		97.5		×	×				×		×	×	×	×	×	×	×	×	×		×				×	
		100.0			×				×	×	×	×	×	×	×	×	×	×	×		×				×	
CI		102.2		×	×				×	×	×	×	×	×	×	×	×	×	×			×			×	
		106.0		×	×	×		×	×	×		×	×	×	×	×	×	×	×		×		×		×	
		110.0	×	×							×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	
SANTONIAN			×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×							

[illegible]

TABLE 2

Distribution of ostracod species in samples from the Campanian and Maastrichtian of Zululand (outcrops at Monzi, Mfolozi River, and Nibela, and borehole BH-9 at Richards Bay) and Agulhas Bank (sample 818).

TABLE 2
Distribution of ostracod species in samples from the Campanian and Maastrichtian of Zululand (outcrops at Monzi, Mfolozi River, and Nibela, and borehole BH-9 at Richards Bay) and Agulhas Bank (sample 818).

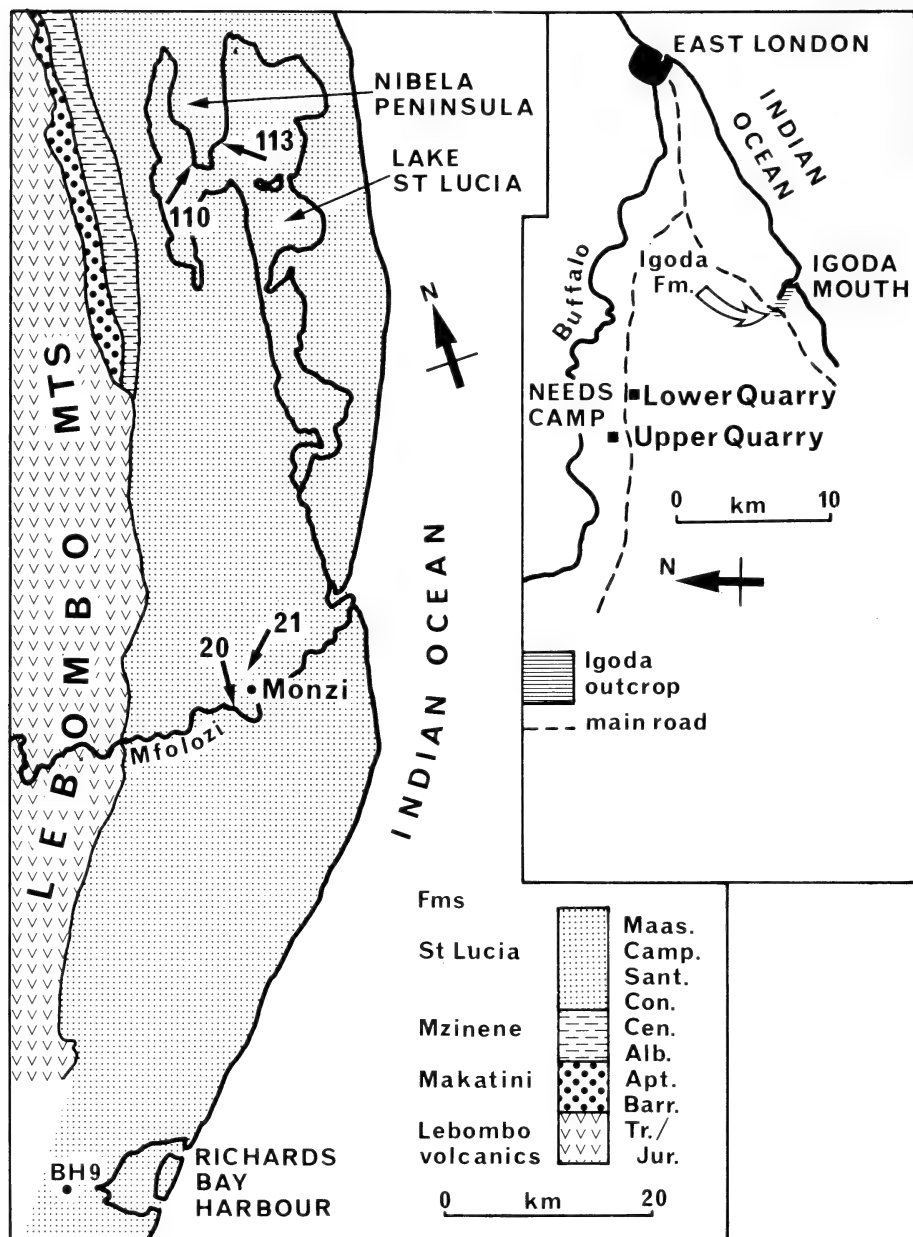


Fig. 2. Main map: details of sampling localities in Zululand. BH-9 is locality 6 in Figures 1 and 3; 20 and 21 are locality 7 in Figures 1 and 3; and 110 and 113 are locality 8 in Figures 1 and 3. Geology is after Kennedy & Klinger (1975). Insert: localities in the vicinity of East London. Lower Quarry Needs Camp, and Igoda estuary are localities 3 and 2, respectively, in Figures 1 and 3.

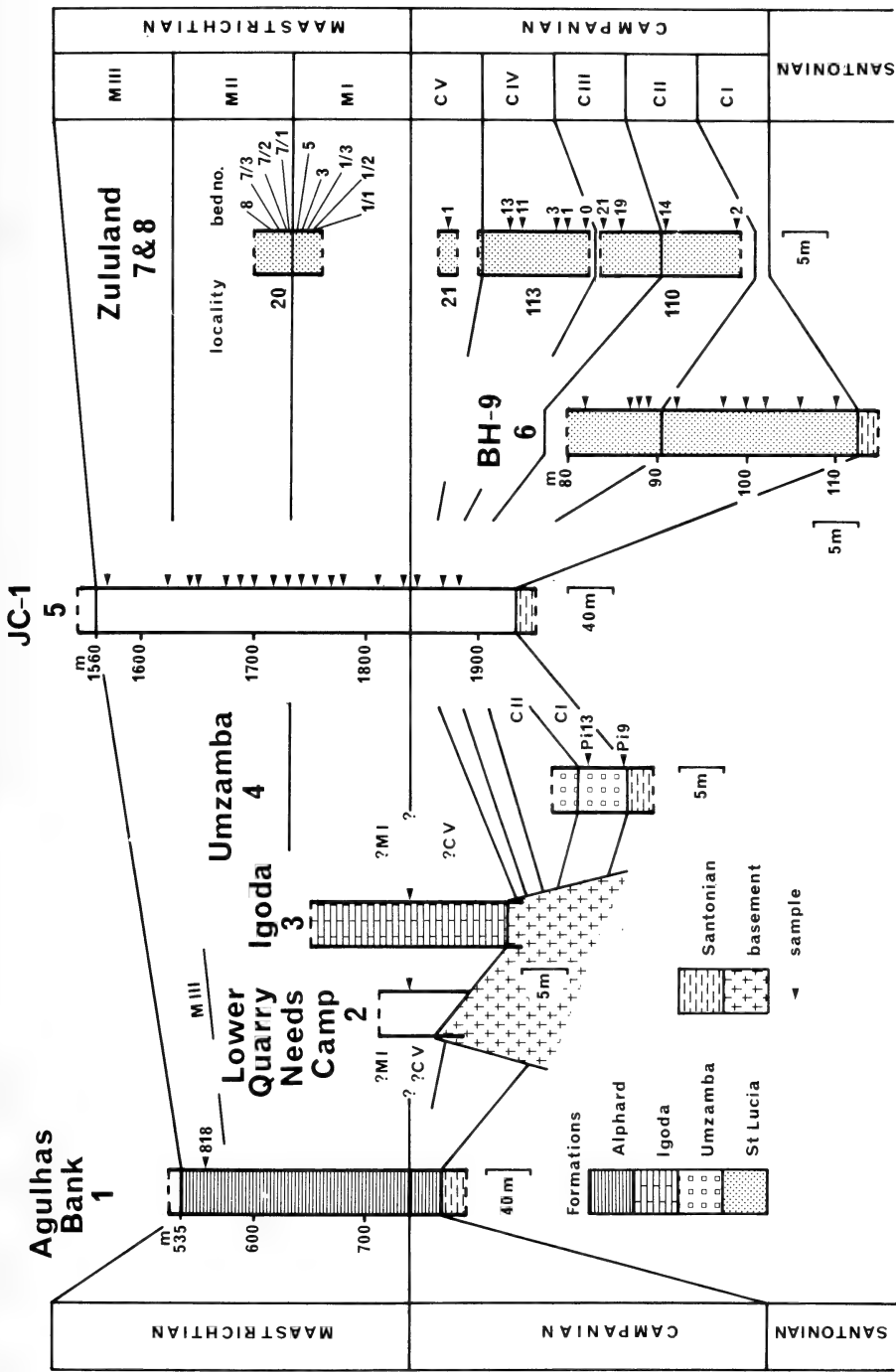


Fig. 3. Measured sections and borehole thicknesses from sampled Campanian–Maastrichtian localities in south-east Africa. Main locality numbers refer to Figure 1, locality and bed numbers in Zululand use the notation and stratigraphy of Kennedy & Klinger (1975). Details of the other sections are after the following authors: BH-9, Dingle (1980); JC-1, Du Toit & Leith (1974); Umzamba, Klinger & Kennedy (1977); Igoda and Needs Camp, Klinger & Lock (1978); Agulhas Bank, borehole Ga A2 type section for Alphard Formation, Du Toit (1976).

rated by McLachlan & McMillan's (1979) recognition of the *R. rugosa* and *G. arca* zones on the Agulhas Bank, and the *G. stuarti* zone in Zululand.

A sample of calcareous sandstone containing *Eubaculites latecarinatus*, *Gunnarites* sp. cf. *G. kalika*, inoceramids, and other indeterminate bivalves has been dredged from Alphard Formation outcrops at 34°08,25'S 25°10,45'E on the Agulhas Bank (Sample 1336; Dingle 1973; Klinger *et al.* 1980). Klinger *et al.* (1980), who described the molluscan fauna, have dated this sample as Maastrichtian I. No ostracods have been recovered from the lithified matrix.

EASTERN CAPE (localities 2–3 on Figs 1, 3)

Small outcrops of late Campanian/early Maastrichtian limestones occur at Igoda (locality 2) and Needs Camp (Lower Quarry) (locality 3).

At Igoda, on the coast (Fig. 2), Klinger & Lock (1978) have described 20 m of glauconitic arenaceous limestones and calcareous sandstones with a basal conglomerate resting on Permo–Triassic Beaufort Group. There is a meagre and poorly preserved invertebrate macrofauna with *Baculites subanceps* Haughton, *Eupachydiscus?* sp. and *Saghalinites* sp. cf. *S. cala* (Forbes) that indicates a late Campanian/early Maastrichtian age.

The Lower Quarry at Needs Camp lies about 13 km inland from Igoda (Fig. 2), and consists of friable, polyzoa-rich limestone with poorly preserved micro- and macrofauna. On the basis of the common presence of the brachiopod *Eolacazella affine* (Bosquet), Klinger & Lock (1978) consider the Lower Quarry and Igoda strata to be the same age, a view corroborated by Siesser & Miles (1979: 148) using calcareous nannofossils. McGowran & Moore (1971) had previously suggested a Campanian to Maastrichtian age for the Needs Camp strata on the presence of two specimens of *Rugoglobigerina* aff. *R. rugosa* (Plummer). Chapman's (1916) type material from Needs Camp (South African Museum slide SAM–2736) has been examined and the specimens re-illustrated herein.

Limestones from both Igoda and Needs Camp are recrystallized, so that the preservation of microfossils is generally poor.

UMZAMBA (locality 4 on Figs 1, 3)

Numerous publications have described the succession and fauna of the coastal cliffs around the Umzamba River mouth in northern Transkei, the most comprehensive and up to date for our purposes being Klinger & Kennedy (1977, 1980), and Makrides (1979). The Campanian I–Santonian III boundary occurs in the cliff section between beds 7 and 8 (within bed 7 according to Makrides 1979) and the section extends into Campanian II (with *Baculites sulcatus*). Chapman (1904, 1923) and Dingle (1969) have described the ostracods from the basal (Santonian) part of the Umzamba succession, but no work has been published on the Campanian ostracod faunas. The Campanian part of the Umzamba cliffs is badly decalcified and only two samples from this section contained ostracods.

OFF-SHORE NATAL, TUGELA CONE (locality 5 on Figs 1, 3)

This is the SOEKOR borehole JC-1 on the continental shelf at 29°27,69'S 31°35,66'E in 72 m of water. The borehole penetrated about 2 300 m of Tertiary and Upper Cretaceous strata before entering Palaeozoic quartzites, and the section between 1 935 m and 1 560 m was reckoned to be Campanian (94 m) and Maastrichtian (281 m) in age (Du Toit & Leith 1974). Eighteen samples containing ostracods were available for study.

ZULULAND (localities 6-8 on Figs 1, 3)

This is the area from which Kennedy & Klinger (1975 et seq.) have collected extensively during the course of their revision of the Cretaceous ammonite faunas of south-east Africa. Here, the Campanian-Maastrichtian strata constitute the upper part of the St Lucia Formation. The southernmost section is in the Richards Bay borehole (BH-9) (28°48,65'S 31°57,75'E, Fig. 2, locality 6 on Figs 1, 3) where approximately 50 m of Campanian I and II overlies 45 m of Santonian which in turn rests on granitic basement. The ammonite stratigraphy of BH-9 has been described by Klinger & Kennedy (1977) and the ostracods by Dingle (1980), who examined ten samples in the 32 m of core available to him from the Campanian I and II. The excellent preservation of the fossils and completeness of the sequence allow BH-9 to be used as a standard for biostratigraphic and palaeoecological comparisons in Zululand and elsewhere.

TABLE 3

Kennedy & Klinger's (1975) ammonite subdivision of the Campanian and Maastrichtian stages in Zululand.

MAASTRICHTIAN

MAASTRICHTIAN III. No ammonites present. Inoceramid debris is abundant.

MAASTRICHTIAN II. Coarsely ornamented baculitids of the *Eubaculites ootacodensis* type are abundant. Pachydiscids are also present.

MAASTRICHTIAN I. Feebly ornamented to smooth *Eubaculites* are common. Other ammonites include *Saghalinites* sp., *Pachydiscus* (*Neodesmoceras*), *Menuites*, '*Epiphyloceras*' and *Hoploscaphites*. The local base is drawn below the appearance of abundant *Eubaculites*.

CAMPANIAN

CAMPANIAN V. Giant *Bostrychoceras* are abundant, with scarcer *Saghalinites* and compressed pachydiscids.

CAMPANIAN IV. *Saghalinites cala* and *Pachydiscus* (*P.*) sp. are common. Other ammonites include *Gunnarites antarcticus*, *Nostoceras*? sp., *Pachydiscus* (*Neodesmoceras*) sp.

CAMPANIAN III. Faunas are sparse but distinctive. A feebly nodose *Baculites* is abundant, and giant (1 m) pachydiscids (probably *Eupachydiscus*) are very common.

CAMPANIAN II. *Menabites* (*Australiella*) is abundant in the lower part of this division but species including *M. (A.) australis* and *M. (A.) besairei*, together with *Bevahites* spp range throughout. *Baculites sulcatus* is abundant throughout, whilst pachydiscids become common in the higher parts: e.g. *Anapachydiscus subdulmensis*, *A. wittekindi*, *A. arrialoorensis* and *Pachydiscus manambolensis*. Other ammonites include *Hoplitoplacenticeras plasticum plasticum*, *Maorites* sp., *Neogaudryceras* sp., *Gaudryceras* sp. and *Bostrychoceras* sp.

CAMPANIAN I. *Submortonicerases woodsi* (Spath) and related forms are common; other ammonites include *Bevahites* spp. and *Menabites* spp, *Hauericeras gardeni*, *Pseudoschloenbachia*, *Bostrychoceras* spp, *Vendegiesiella* sp. cf. *spinosa*, *V. trituberculata*, *Karapadites*, and diplomoceratids. The local base is drawn below the level of abundant *Submortonicerases*.

Upper Campanian II to Campanian IV sections are exposed in extensive cliffs along the southern part of the Nibela Peninsula in the St Lucia Game Park (locality 8 on Figs 1, 3; sites 110, 113 on Fig 2). Upper Campanian II to Campanian III material was collected at Kennedy & Klinger's (1975) locality 110 (27°59,17'S 32°24,57'E), whilst the Campanian IV was sampled at their locality 113 (27°58,20'S 32°26,95'E). Farther south, upper Campanian to Maastrichtian sections are exposed in the vicinity of the village of Monzi (locality 7 on Figs 1, 3). Campanian V was sampled in a road cutting to the north of the village (Kennedy & Klinger's (1975) locality 21, 28°25,00'S 32°18,58'E) (Fig. 2), whilst Maastrichtian I and II occurs in a complete sequence in low cliffs on the north bank of the Mfolozi River, and in a small quarry 200 m to the east (Kennedy & Klinger's (1975) locality 20, 28°26,98'S 32°16,60'E) (Fig. 2). Although the upper parts of some sections are heavily decalcified, the preservation of microfossils in the unweathered sections is generally moderate to good.

A total of 53 fossiliferous samples (including Chapman's (1916) types from Needs Camp) were available for study. Microfossils were extracted by washing, and photographed with a Cambridge 180 Stereoscan. Specimens were mounted on aluminium stubs using double-sided Sellotape and were coated with a gold palladium mixture. Types and illustrated material are deposited in the South African Museum, Cape Town.

SYSTEMATIC DESCRIPTIONS

The classification used here is based mostly on the Ostracod *Treatise* (Moore 1961), with various additions necessitated by recent work. Morphological terms have been supplemented by those introduced to cover features visible at high magnifications (e.g. Sylvester-Bradley & Benson 1971). In addition to taxonomic notes, age range, geographic distribution and palaeoecology for each species are discussed, with ecological preferences expressed in terms of ostracod assemblages 1 to 7, and the sedimentary environments that they are thought to represent. These assemblages are defined in the discussion section.

Abbreviations: RV = right valve, LV = left valve, MPC = marginal pore canals, SCT = subcentral tubercle, ATE = anterior terminal element, PTE = posterior terminal element, ME = median element, AM = anterior margin, PM = posterior margin, DM = dorsal margin, VM = ventral margin, NPC = normal pore canals, and MA = marginal areas.

Subclass OSTRACODA Latreille, 1806
Order PODOCOPIDA Müller, 1894
Suborder PLATYCOPINA Sars, 1866
Family *Cytherellidae* Sars, 1866

Members of this family constitute one of the main elements of the Campanian-Maastrichtian ostracod faunas of south-east Africa, particularly in the

TABLE 4
Environmental distribution of selected genera and species from Monzi, Mfolozi, Nibela and BH-9, Zululand.

estimated water depths (metres)	restricted					unstable					stable				
	shallow	circu- lation	open	200	200-300	300-500	>500	>500	>500	>500	>500	>500	>500	>500	>500
Cytherellidae															
<i>Cytherelloidea umzambaensis</i>
<i>C. contorta</i>
<i>C. griesbachi</i>
<i>C. mfoloziensis</i>
<i>Cytherella</i> sp. (morpho. types)
<i>Platella africana</i>
Bairdiacea															
<i>Bythocypris richardsbayensis</i> (mean % total ostracoda)
<i>Bairdopillata andersoni</i> (mean % total ostracoda)
Cypridacea															
<i>Paracypris</i> spp (mean % total ostracoda)
<i>Pontocyprilla nibelaensis</i>
Cytheracea															
<i>Unicapella sacsi</i>
<i>Haughtonileberis haughtoni</i>
<i>H. fissilis</i>
<i>H. vanhoepeni</i>
<i>H. nibelaensis</i>
<i>Oerthella pennata</i>
<i>O. sp. A</i>
<i>O. africana</i>
<i>O. maastrichtia</i>
<i>Cythereis klingerii</i> (mean % Cytheracea)
<i>Hermanites kennedyi</i>
<i>H? arcus</i>
<i>Trachyleberis zululandensis</i>
<i>Paracythereis monziensis</i>
<i>Amphicytherura tumida</i>
<i>A. zululandensis</i>
<i>A. sp. A</i>
<i>A. armatus</i>
<i>Xestoleberis lucianensis</i> (mean % Cytheracea)
<i>Brachycythere longicaudata</i> (mean % Cytheracea)

* — present

** — preferred environment

+ — large standard deviation

areas of Zululand north of the Richards Bay BH-9 borehole. In the Campanian I, cytherellid populations make up 10–20 per cent of the total fauna and this rises in Campanian II: 20–35 per cent (Richards Bay borehole) to ~20 per cent (at outcrop farther north). Campanian III ostracod faunas are also about 20 per cent cytherellid, but this increases rapidly in Campanian IV, V, and lower Maastrichtian I to reach levels up to 50 per cent, falling to 20–30 per cent in Maastrichtian II. As will be noted in the discussion section, these fluctuations are directly related to changes in the palaeosedimentary environments.

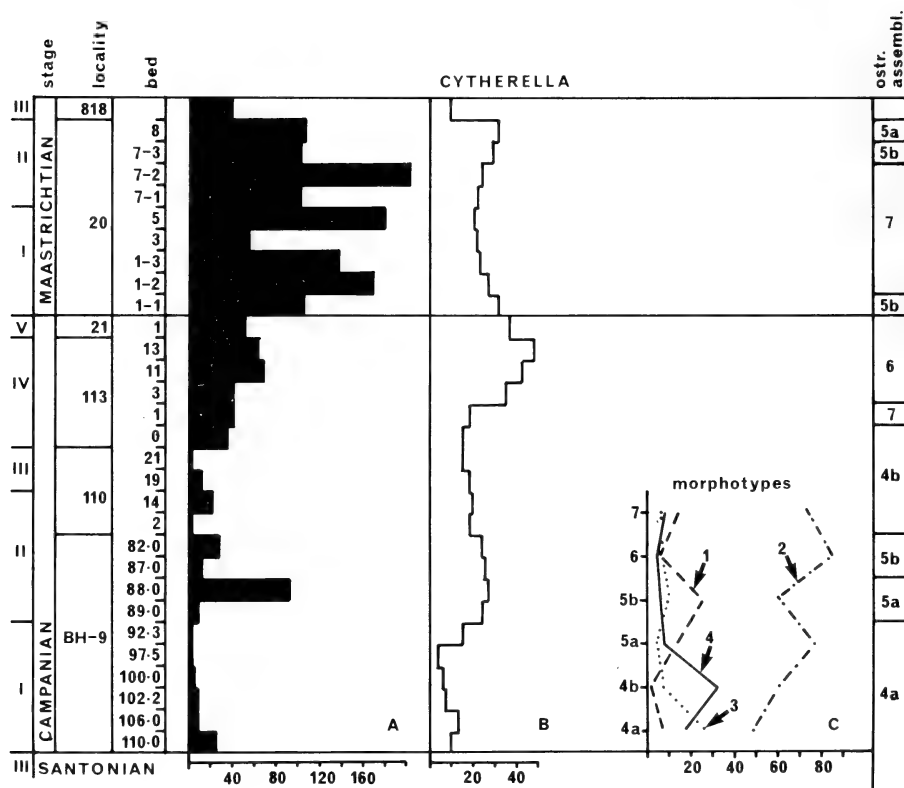


Fig. 4. Distribution of *Cytherella* sp. in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves. B. Percentage of total ostracod population. C. Morphotypes 1–4 as percentage of total *Cytherella* sp. plotted by ostracod assemblage.

The family is represented in the Campanian–Maastrichtian by 3 genera: *Cytherella*, *Cytherelloidea*, and *Platella* with 5 designated species and 4 morphotypes. 2 of the species and all 4 morphotypes are inherited from the Santonian, whilst 1 species is restricted to the Campanian (*Cytherelloidea griesbachi*), and 2 are restricted to the Campanian–Maastrichtian (*Cytherelloidea mfoloziensis* and *Platella africana*).

Genus *Cytherella* Jones, 1849*Cytherella* sp.

Fig. 5A–F

Cytherella sp. 1, 2, 3, 4, Dingle, 1980: 5–7, fig. 2A–F.*Remarks*

Dingle (1980) recognized four morphotypes of *Cytherella* in the Richards Bay BH–9 borehole and it was hoped that with the addition of more material formal descriptions of these might be possible. Whilst all four have been recognized in younger samples, and estimates of their relative importance have been made (Fig. 4C), it has not been possible confidently and consistently to discriminate to the extent of formally describing new species. 'End members' of each morphotype can easily be recognized but within any population there is usually a considerable residue of intermediate forms. For the purposes of population counts, these can be placed in categories, but the decision is sometimes arbitrary. Consequently no formal subdivision within the genus *Cytherella* is yet possible.

Age, distribution, palaeoecology

Santonian II to Maastrichtian III (Zululand outcrops, BH–9 Richards Bay, Igoda, JC–1 borehole, Agulhas Bank). Although *Cytherella* sp. occurs in ostracod assemblages 1–3, 4a, 4b, 5a, 5b, 6–7, it is only consistently present in numbers above trace in 4–7, reaching a maximum (>40% total ostracod population) in 6 (Fig. 4): deep (>500 m, outer shelf/upper slope) oceanographically unstable environment.

In terms of the four morphotypes recognized by Dingle (1980), Figure 4C shows mean percentage of total *Cytherella* plotted against the various ostracod assemblages. Several points emerge:

- (i) Morphotype 2 (ovate form) dominates throughout (48–84%) but is most prominent in assemblages 6, 7, and 5a (>60%).
- (ii) Morphotypes 3 (elongate, parallel sided form) and 4 (large plump form) in combination are most common in assemblages 4a and 4b.
- (iii) Morphotype 1 (asymmetric form) is consistently most abundant in the ostracod assemblages 5a and 5b.

Based on their *preferred* habitat, therefore, it is possible to recognize the following approximate groupings: 100–200 m—morphotypes 3 and 4; 200–500 m—morphotype 1; >500 m—morphotype 2.

Cytherella sp. occurs in small numbers (dominantly carapaces) in the Maastrichtian part of borehole JC–1 (between levels 1 835 and 1 652 m) (Table 10). Morphotypes 2 and 3 have been recognized, but because of their scarcity no environmental significance can be placed on their presence. It is probably significant, however, that *Cytherella* sp. is virtually absent from samples in which charophytes has been found, and this is thought to reflect the species' intoler-

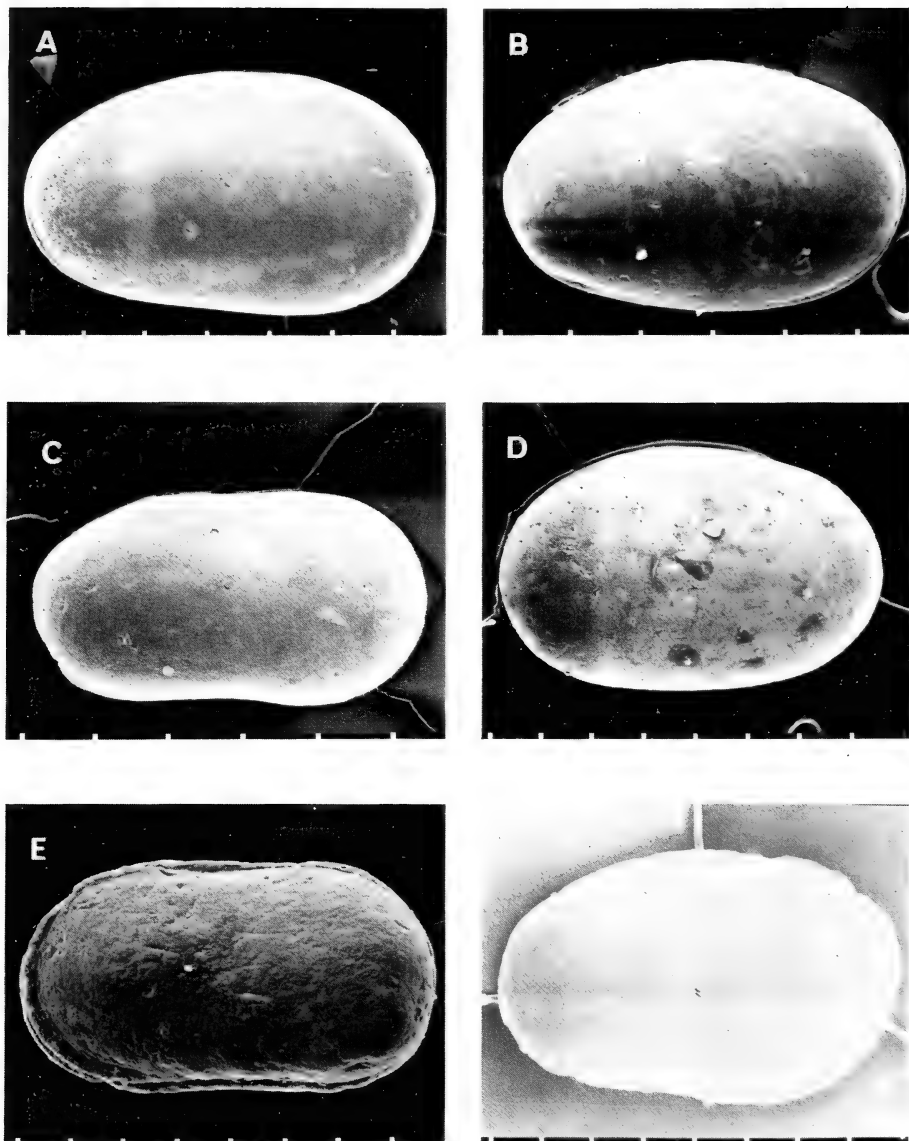


Fig. 5. *Cytherella*. A. *Cytherella* sp. morphotype 1, SAM-K5568, BH9 82,03 m, RV, Campanian II. B. *Cytherella* sp. morphotype 2, SAM-K5569, BH9 82,03 m, RV, Campanian II. C. *Cytherella* sp. morphotype 3, SAM-K5570, BH9 82,03 m, RV, Campanian II. D. *Cytherella* sp. morphotype 4, SAM-K5571, BH9 82,03 m, RV, Campanian II. E. *Cytherella* sp. morphotype 3, SAM-K5662, JC-1 1811 m, LV, Maastrichtian. F. *Cytherella* sp. morphotype 2, SAM-K5663, JC-1 1835 m, RV, Maastrichtian.

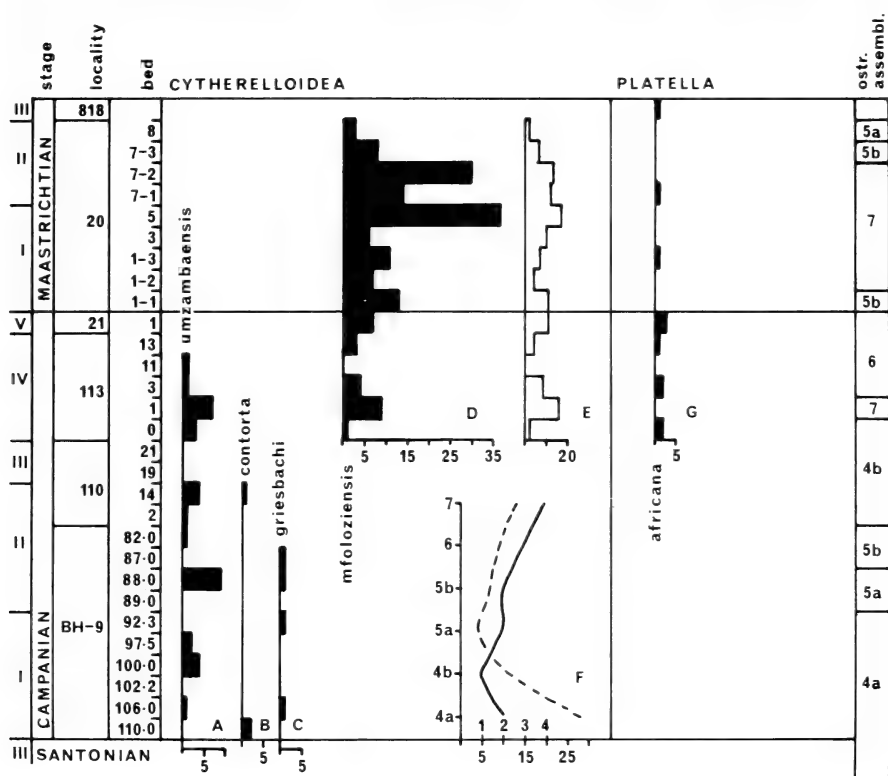
Scale bars all 100 μ .

ance to large influxes of freshwater-derived detritus. A similar antipathetic relationship has been noted for *Bythocypris*? sp. in borehole JC-1.

Genus *Cytherelloidea* Alexander, 1929

This is an important subsidiary genus in some of the Upper Cretaceous rocks of south-east Africa. It is recorded sporadically throughout the Santonian II to Maastrichtian II of Zululand and Richards Bay BH-9 borehole where it generally constitutes 1-5 per cent of the total ostracod population, but has not been found in the following areas: the Maastrichtian III of the Agulhas Bank; the late Campanian/early Maastrichtian of Igoda and Needs Camp; Campanian-Maastrichtian of the JC-1 borehole.

In the Campanian–Maastrichtian sequences of Zululand, *Cytherelloidea* is represented by four species: *C. umzambaensis*, *C. contorta*, *C. griesbachi*, and



C. mfoloziensis. The genus is always numerically subordinate to its relation *Cytherella*, but reaches its maximum importance in terms of percentage of the family Cytherellidae in ostracod assemblage 4a (28%), whilst constituting <10 per cent in assemblages 5a, 5b and 6 (Fig. 6). These data indicate that in south-east Africa *Cytherelloidea* is generally more tolerant of shallower water conditions than is *Cytherella*, although its preferred environment is also deep water (>500 m, outer shelf/upper slope), where its mean percentage of the total ostracod population reaches 3–4 per cent, compared to 1–2 per cent in the shallower areas.

Cytherelloidea umzambaensis Dingle, 1969

Figs 7A, 9C

?*Cytherella williamsoniana* Jones, 1849, Chapman, 1904: 236.

Cytherelloidea umzambaensis Dingle, 1969: 351–353, fig. 3. Dingle 1980: 7, figs 3A, 4A–B.

Remarks

The range of *C. umzambaensis* overlaps with that of *C. mfoloziensis* in Campanian IV and it would seem that the latter evolved from the former under the stress of the establishment of deep-water environments in lower Campanian IV times. In late Campanian IV, *C. umzambaensis* declines in importance before it is finally replaced (Fig. 6).

Age, distribution, palaeoecology

Santonian II to Campanian IV (Umzamba, Richards Bay BH–9 borehole, and Nibela Peninsula). *C. umzambaensis* is an environmentally tolerant species that occurs sporadically and in relatively small numbers in the Richards Bay BH–9 borehole and at outcrops in the Nibela Peninsula. It has been found in ostracod assemblages 1–3, 4a, 4b, 6–7 but preferred the moderate depth environments represented by assemblages 4a, 4b and 5a: quiet, 100–300 m, inner-outer shelf environments (Table 4).

Cytherelloidea contorta Dingle, 1980

Fig. 7B

Cytherelloidea contorta Dingle, 1980: 11–12, figs 3D, 4E.

Remarks

This rare species has been recorded from single horizons in the Richards Bay BH–9 borehole and at outcrop in the Nibela Peninsula (Fig. 6B).

Age, distribution, palaeoecology

Campanian I and Campanian II (Richards Bay BH–9 borehole and Nibela Peninsula). *C. contorta* is environmentally bound to ostracod assemblage 4a and 4b: quiet water, moderate depths (?100–200 m, inner-mid shelf).

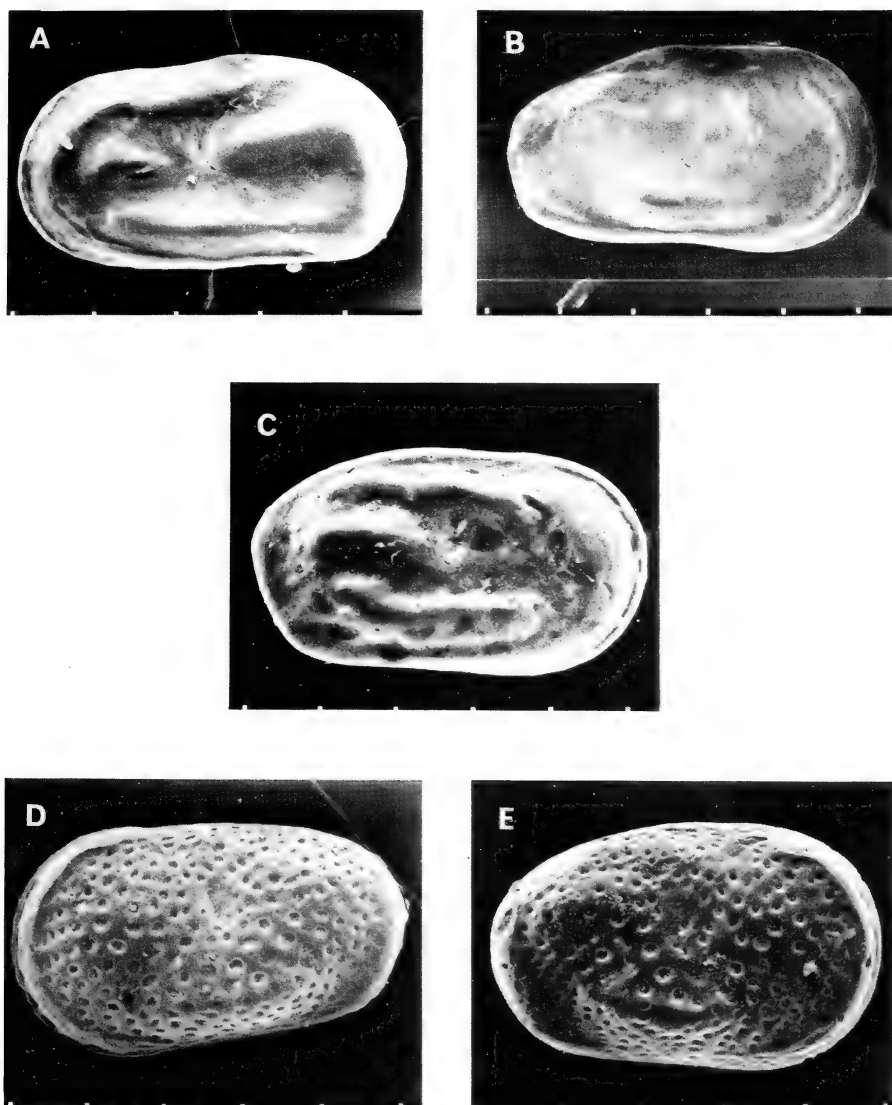


Fig. 7. A. *Cytherelloidea umzambaensis* Dingle, 1969, SAM-K5573, BH9 106,0 m, LV, Campanian I. B. *Cytherelloidea contorta* Dingle, 1980, SAM-K5576, BH9 110,0 m, RV, Campanian I. C. *Cytherelloidea griesbachi* Dingle, 1980, SAM-K5575, BH9 88,39 m, RV, Campanian II. D. *Platella africana* sp. nov., holotype, SAM-K5669, locality 21-1, Monzi, LV, Campanian V. E. *Platella africana* sp. nov., SAM-K5670, locality 113-0, Nibela Peninsula, RV, Campanian IV.
Scale bars all 100 μ .

Cytherelloidea griesbachi Dingle, 1980

Fig. 7C

Cytherelloidea griesbachi, Dingle, 1980: 10–11, figs 3B, 4D.*Remarks*

This rare species has not been encountered outside the Richards Bay BH–9 borehole.

Age, distribution, palaeoecology

Upper Santonian III to Campanian II (Richards Bay BH–9 borehole). *C. griesbachi* occurs in ostracod assemblages 3, 4a and 5a and 5b, but the small numbers available do not allow a precise assessment of its environmental preference. However, because it is restricted to the deeper water populations in assemblage 3, *C. griesbachi* was probably confined to quiet, moderate to deep-water environments (~100–500 m, inner-outer shelf).

Cytherelloidea mfoloziensis sp. nov.

Figs 8A–E, 9A–B

Derivation of name

Locality of type.

Holotype

SAM–K5664, LV, locality 20–7/1, Mfolozi River, Maastrichtian II

Paratypes

SAM–K5665, RV, locality 20–7/1, Mfolozi River, Maastrichtian II

SAM–K5666, LV, locality 113–3, Nibela, Campanian IV

SAM–K5667, RV, locality 113–3, Nibela, Campanian IV

SAM–K5668, LV, locality 20–7/1, Mfolozi River, Maastrichtian II

Diagnosis

Species with three longitudinal ribs and a prominent AM rim. The most conspicuous feature is a concave-upward ventrolateral ridge.

Description

External features. In lateral view rectangular. AM symmetrically rounded, PM truncated in females, rounded but posterodorsally truncated in males. DM generally straight but with slight concavity in front of mid point. VM straight to slightly concave. Surface ornamented with three longitudinal ribs and a wide AM rim. The latter merges into the VM and DM, but is not connected to the other longitudinal elevations. Dorsal rib is curved and ventrally deflected at about quarter length, in some specimens its anterior end merges with the median rib; it rises posteriorly and joins the valve margin posterodorsally. The median

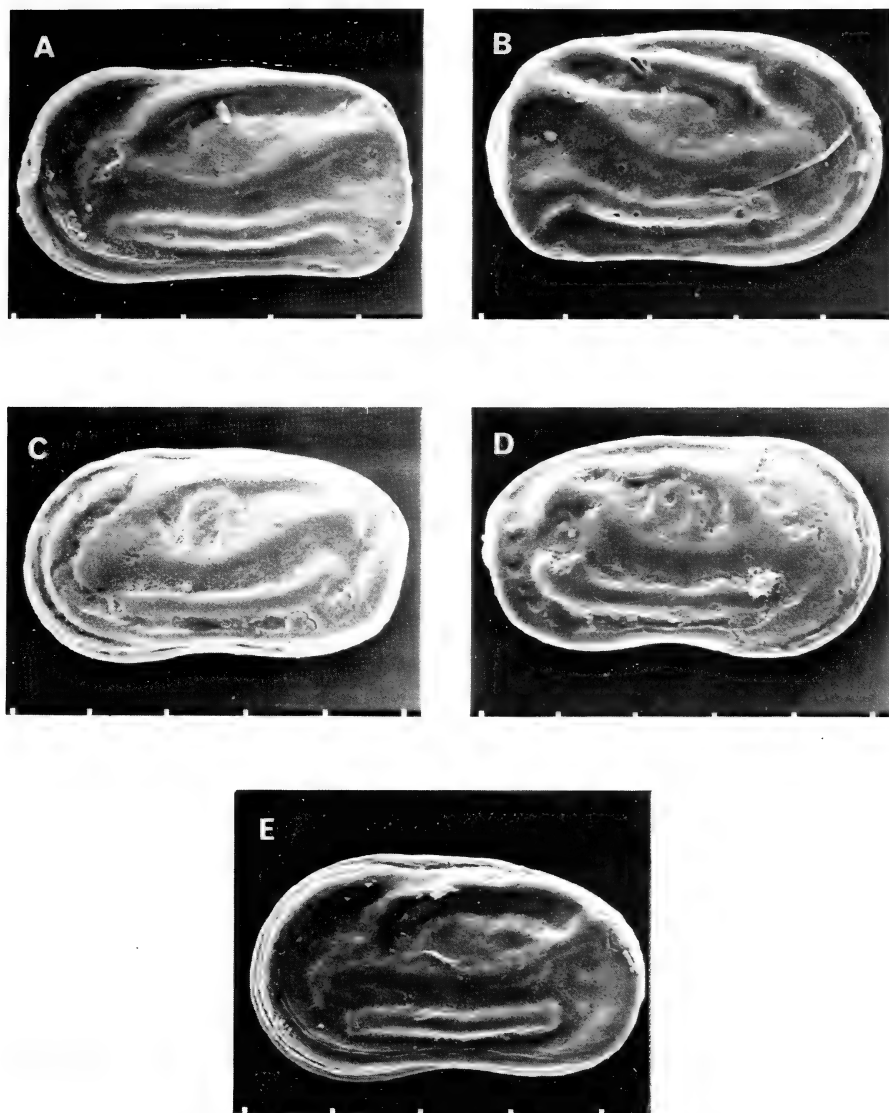


Fig. 8. *Cytherelloidea mfoloziensis* sp. nov. A. Holotype, SAM-K5664, locality 20-7/1, Mfolozi River, LV, Maastrichtian II. B. SAM-K5665, locality 20-7/1, Mfolozi River, RV, Maastrichtian II. C. SAM-K5666, locality 113-3, Nibela Peninsula, LV, Campanian IV. D. SAM-K5667, locality 113-3, Nibela Peninsula, LV, Campanian IV. E. SAM-K5668, locality 20-7/1, Mfolozi River, LV, Maastrichtian II.

Scale bars all 100 μ .

rib runs from the posterodorsal corner to the mid point where it is deflected horizontally; it frequently swells anteriorly. The ventral rib is short and concave dorsally; in males it is not attached at its extremities, but in females merges with a posteroventral swelling.

Internal features. No internal views seen.

Remarks

C. mfoloziensis has a similar rib pattern to *C. umzambaensis* (Fig. 9) and it is suggested that the former evolved from the latter in lowermost Campanian IV. The two can be distinguished by the prominence of the curved ventrolateral rib and distinct separation of the AM and dorsal ribs in *C. mfoloziensis*, and the more bulbous nature of the posterior ends of the dorsal and ventral ribs of *C. umzambaensis*. *C. mfoloziensis* is an important subsidiary species in the Maastrichtian faunas where it constitutes up to 17 per cent of the cytherellid element (5% total ostracod fauna).

Dimensions (mm)

	length	height
K5664	0,45	0,25
K5665	0,47	0,28
K5666	0,50	0,28
K5667	0,50	0,28
K5668	0,45	0,25

Age, distribution, palaeoecology

Campanian IV to Maastrichtian II (Nibela, Monzi and Mfolozi areas, Zululand). *C. mfoloziensis* occurs in ostracod assemblages 4b, 5a, 5b, 6–7, indicating that it tolerated a variety of medium to deep water environments (Fig. 6, Table 4). However, it preferred the deep (>500 m outer shelf/upper continental slope) stable conditions represented by ostracod assemblage 7.

Genus *Platella* Coryell & Fields, 1937

Platella africana sp. nov.

Fig. 7D–E

Derivation of name

Locality of type.

Holotype

SAM-K5669, LV, locality 21–1, Monzi, Campanian V

Paratypes

SAM-K5670, RV, locality 113–0, Nibela, Campanian IV

SAM-K5671, LV, locality 113–0, Nibela, Campanian IV

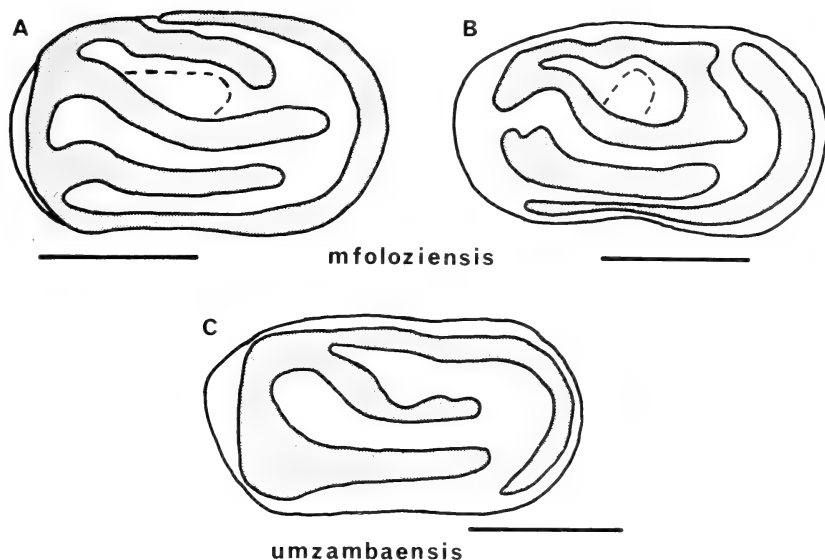


Fig. 9. Sketches of *Cytherelloidea* species, right valves, with positive features shaded.
 A. *C. mfoloziensis* sp. nov., SAM-K5665, locality 20-7/1, Mfolozi River, Maastrichtian II.
 B. *C. mfoloziensis* sp. nov., SAM-K5667, locality 113-3, Nibela Peninsula, Campanian IV.
 C. *C. umzambaensis* Dingle, 1969, BH9 120,22 m, Santonian III.
 Scale bars all 300 μ .

Diagnosis

Species with curved ventrolateral and rounded posterodorsal swellings.

Description

External features. In lateral view, asymmetrically ovate. AM broadly and symmetrically rounded, PM asymmetrically rounded, truncated ventrally. DM weakly convex, VM straight. There is a narrow AM rim and a broad posteroventral marginal elevation. Central area has short, curved ventrolateral and rounded, posterodorsal swellings. There is a median sulcus at about mid length and within this the impressions of the adductor MS are clearly visible; they consist of a curved double row of six elliptical scars—the typical ‘feather’ shape associated with the genus *Cytherella*. Surface covered overall with coarse, widely spaced ovate fossae, in some areas (e.g. adjacent to the AM rim) forming a reticulate pattern.

Internal features. No internal views available.

Remarks

This genus has been recorded from the Campanian of Western Australia by Bate (1972), who illustrated two juveniles in open nomenclature. Our species differs from these in details of surface relief.

Dimensions (mm)

	length	height
K5669	0,50	0,29
K5670	0,49	0,29
K5671	0,47	0,29

Age, distribution, palaeoecology

Campanian IV to Maastrichtian III (Monzi, Mfolozi, and Nibela areas Zululand, and Agulhas Bank). *P. africana* occurs in ostracod assemblages 4b, 6-7, and sample 818 (Fig. 6G). This shows that whilst it always occurs in minor amounts it was moderately environmentally tolerant. It seems to have preferred the deep-water (>500 m outer shelf/upper continental slope) unstable environment represented by ostracod assemblage 6.

Suborder PODOCOPINA Sars, 1866

Superfamily BAIRDIACEA Sars, 1888

The Bairdiacea are one of the most important, and locally dominant, ostracod groups in the Upper Cretaceous of south-east Africa. Present in the Santonian sequences of Richards Bay BH-9 borehole and Umzamba in subsidiary numbers (up to 10% total ostracod population), they suddenly appear in large numbers in the lower Campanian I with the onset of deeper-water sedimentary environments, and rapidly increase through the lower Campanian, replacing the Cytheracea to become the dominant group (40-45% total population) in most of the deeper water habitats. The superfamily is represented by two genera, *Bairdoppilata* and *Bythocypris*, and although both reach their maximum numerical development in the deeper water environments, *Bythocypris* demonstrates the greater environmental tolerance by maintaining a more consistent presence in the harsher (less stable) shallow-water facies represented by assemblages 1 and 2 and the deep-water facies of assemblage 6 (Fig. 10C).

Family **Bairdiidae** Sars, 1888Genus *Bairdoppilata* Coryell, Sample & Jennings, 1935

One of the most important genera in the Campanian-Maastrichtian rocks of south-east Africa, it forms 29 per cent of total fauna (average of six assemblage means) in the Zululand outcrops and BH-9 borehole (>30% in four of the six assemblages), 25 per cent at Igoda, 90 per cent at Needs Camp, 28 per cent in borehole JC-1, and 1 per cent in Agulhas Bank sample 818.

Three species (*B. andersoni*, *B. africana*, *B. sp. A*) and one subspecies (*B. andersoni aequalis*) have been recognized, but only in the shallow water environments of the Transkei Swell does notable mixing appear to have taken place (Table 1). Here, *B. andersoni*, *B. africana*, and *B. sp. A* all occur, whereas in Zululand, BH-9, and JC-1, the faunas are probably monospecific (*B. andersoni* and *B. cf. africana*, respectively).

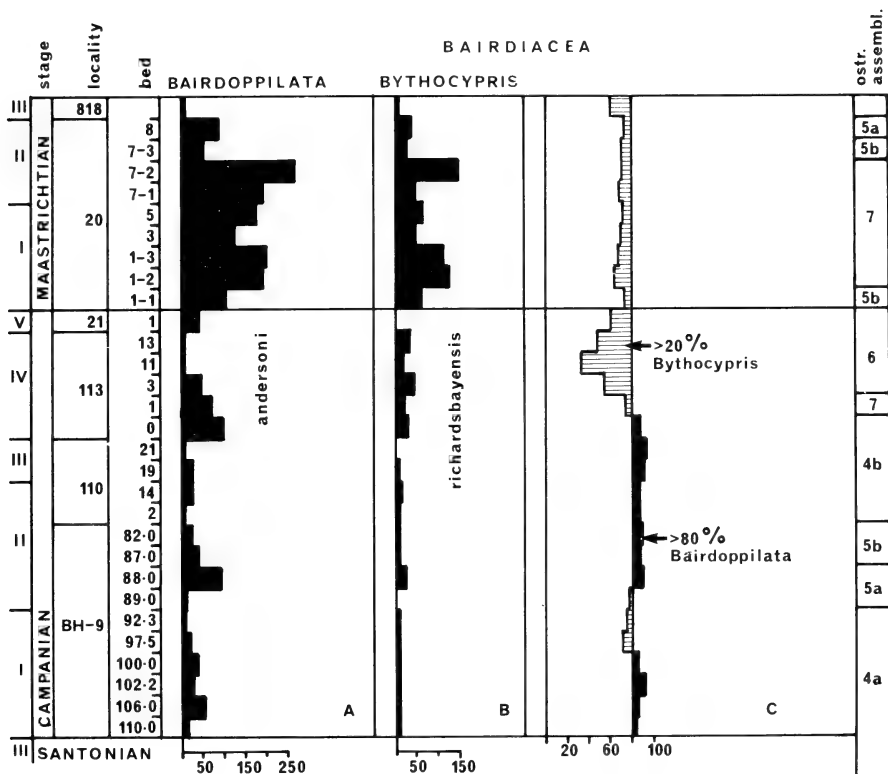


Fig. 10. Distribution of Bairdiacea in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Bairdoppilata andersoni*. B. Total number of valves of *Bythocypris richardsbayensis*. C. *Bairdoppilata andersoni* and *Bythocypris richardsbayensis* as percentage of Bairdiacea.

Bairdoppilata andersoni Dingle, 1980

Figs 11A–D, 13A–B

Bairdoppilata andersoni Dingle, 1980: 12–14, fig. 5A–F.

Remarks

Large numbers of well-preserved valves and carapaces of this robust species have been recovered from Zululand and BH-9 (Fig. 10A), whilst mainly carapaces occur at Needs Camp. *B. andersoni* is numerically the single most important ostracod species in the Campanian–Maastrichtian of south-east Africa, where it dominates (>20%) five of the six ostracod assemblages recognized in the Zululand and BH-9 populations.

Age, distribution, palaeoecology

Santonian II to Maastrichtian III (Richards Bay BH-9 borehole, Zululand outcrops, Igoda, Needs Camp, and Agulhas Bank). *B. andersoni* occurs in all

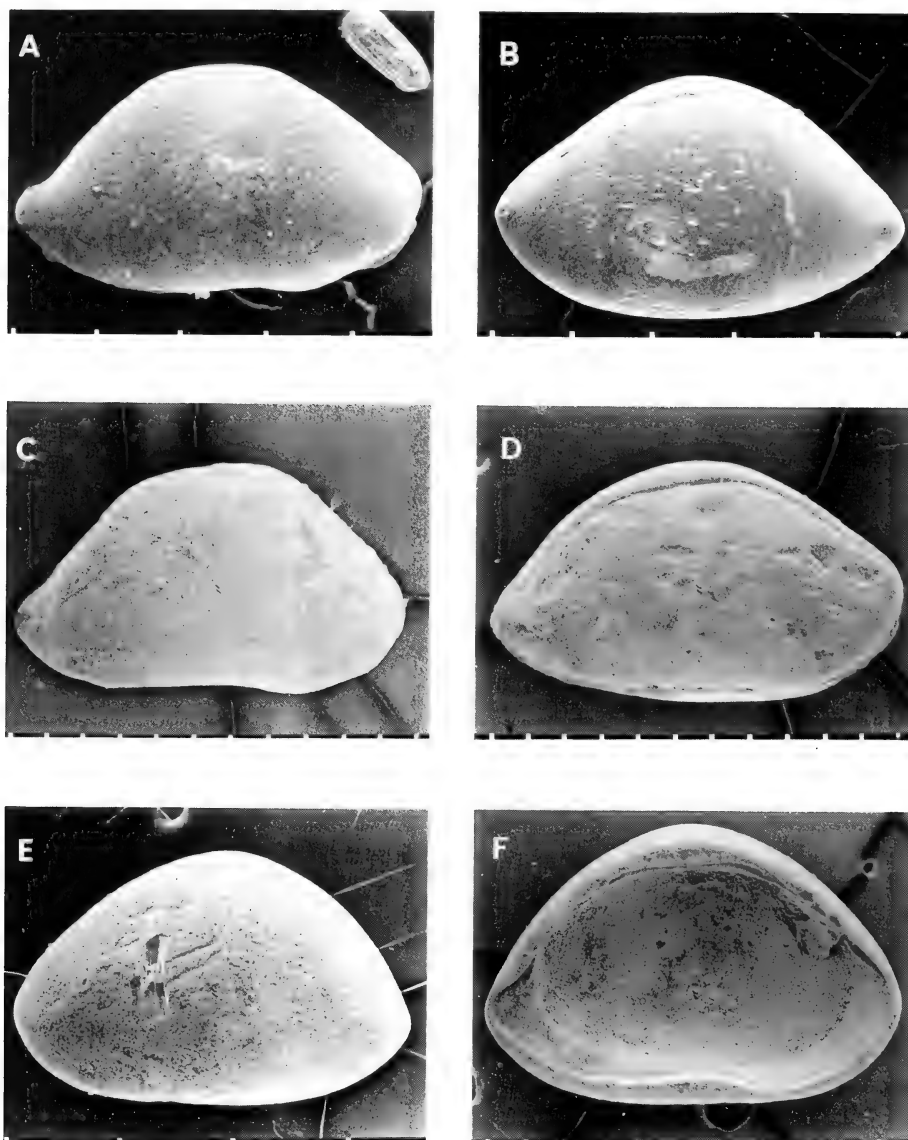


Fig. 11. *Bairdoppilata*. A–D. *B. andersoni* Dingle, 1980. A. SAM-K5577, BH9 88,39 m, RV, Campanian II. B. SAM-K5578, BH9 88,39 m, LV, Campanian II. C. SAM-K5672, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. D. SAM-K5673, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. E. *B. andersoni aequalis* (Chapman, 1916), holotype, SAM-2736/20, Lower Quarry Needs Camp, LV, late Campanian/early Maastrichtian. F. *B. andersoni aequalis* (Chapman, 1916), holotype, SAM-2736/20, Lower Quarry Needs Camp, internal LV, late Campanian/early Maastrichtian.

Scale bars: C–D, F = 100 μ , A–B, E = 300 μ .

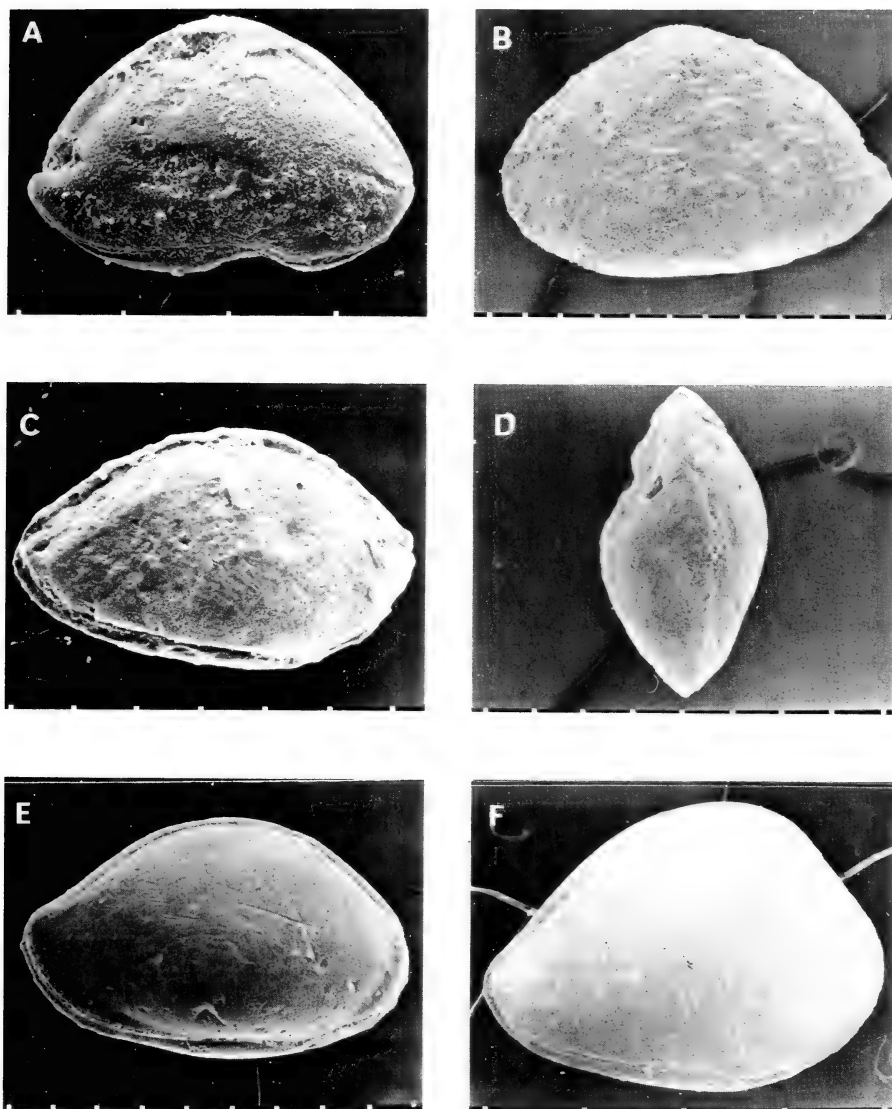


Fig. 12. *Bairdoppilata*. A. *B. andersoni aequalis* (Chapman, 1916), SAM-2736/17, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. B. *B. andersoni aequalis* (Chapman, 1916), SAM-K5674, Lower Quarry Needs Camp, LV, late Campanian/early Maastrichtian. C. *B. africana* (Chapman, 1916), holotype, SAM-2736/19, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. D. *B. africana* (Chapman, 1916), holotype, SAM-2736/19, Lower Quarry Needs Camp, dorsal view, carapace, late Campanian/early Maastrichtian. E. *B. cf. B. africana* (Chapman, 1916), SAM-K5675, JC-1 1625 m, RV, Maastrichtian. F. *B. cf. B. africana* (Chapman, 1916), SAM-K5676, JC-1 1884 m, RV, Campanian.

Scale bars: A, F = 300 μ , others = 100 μ .

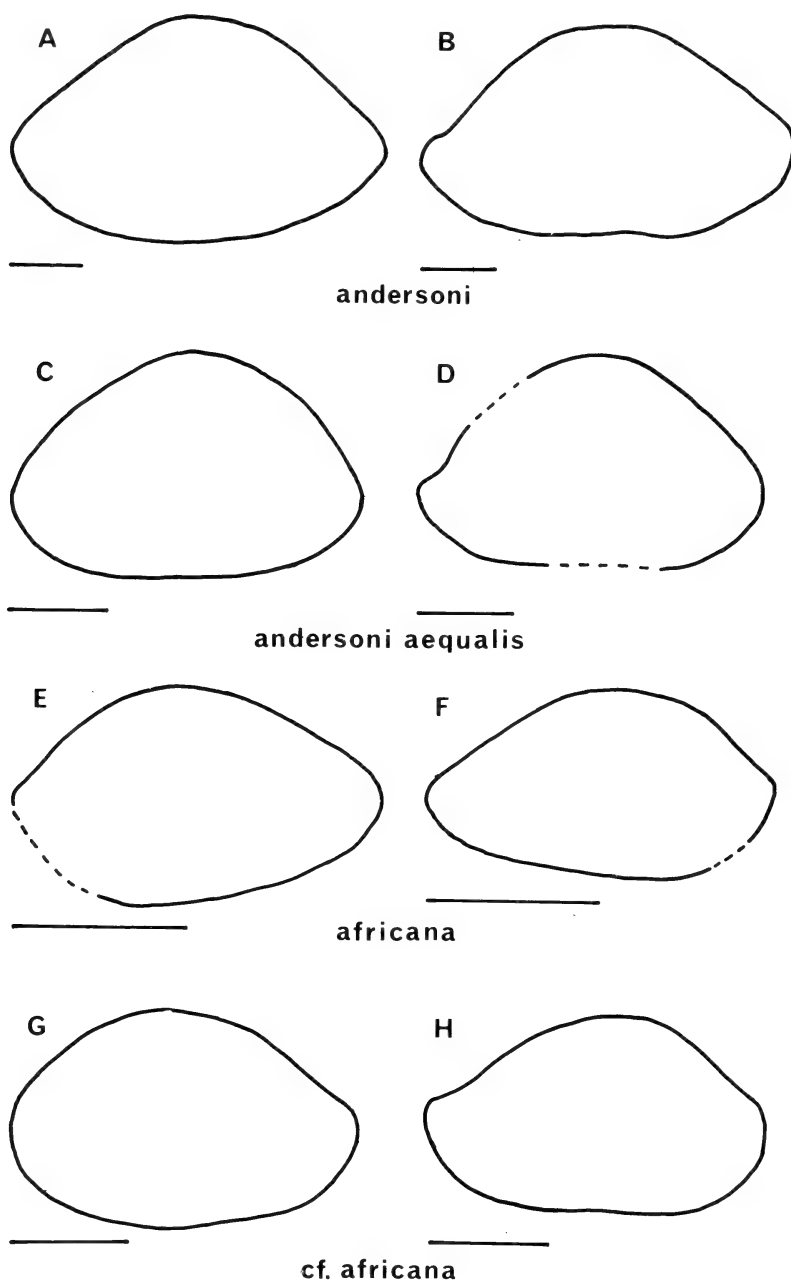


Fig. 13. Sketches of *Bairdoppilata*. A. *B. andersoni* Dingle, 1980, SAM-K5578, BH9 88,39 m, LV, Campanian II. B. *B. andersoni* Dingle, 1980, SAM-K5577, BH9 88,39 m, RV, Campanian II. C. *B. andersoni aequalis* (Chapman, 1916), SAM-2736/20, Lower Quarry Needs Camp, LV, late Campanian/early Maastrichtian. D. *B. andersoni aequalis* (Chapman, 1916), SAM-2736/17, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. E-F. *B. africana* (Chapman, 1916), SAM-2736/19, Lower Quarry Needs Camp, LV(E) and RV(F), late Campanian/early Maastrichtian. G-H. *B. cf. B. africana* (Chapman, 1916), SAM-K5675, JC-1 1625 m, LV(G) and RV(H), Maastrichtian.

Scale bars all 300 μ .

the ostracod assemblages recognized in the Richards Bay–Zululand area, but its environmental preference was for the deeper-water facies, especially 5a and 7 (i.e. water depths >300 m in stable environments) (Table 4).

Bairdoppilata andersoni aequalis (Chapman, 1916)

Figs 11E–F, 12A–B, 13C–D

Bairdia subdeltoidea Münster sp. var. *aequalis* var. nov. Chapman, 1916: 115, pl. XV, fig. 17a–b. (SAM–2736/20.)

Bairdia subdeltoidea Münster, Chapman, 1916: 114–115 (no illustration). (SAM–2736/17.)

Remarks

Two specimens of this subspecies occur in slide SAM–2736. Square 18 is obviously the holotype illustrated by Chapman (1916, fig. 17a–b) and square 17 is probably the carapace referred to *Bairdia subdeltoidea* by Chapman, but not illustrated.

These specimens have been retained here within a subspecific allocation because they differ subtly but significantly in outline from typical examples of *Bairdoppilata andersoni* s.s. These differences are shown in Figure 13 and can be summarized as: a straighter VM (particularly in LV), and a more rounded DM (RV) in subspecies *aequalis*. Consequently, *andersoni* s.s. has a more almond-like outline in lateral view. MS in the two varieties are, however, almost identical.

The ‘deep sinus’ on the VM of specimen SAM–2736/17 recorded by Chapman (1916) is merely a result of damage to the carapace. Small teeth are clearly visible on the hinge of the holotype, which is remarkably well preserved in comparison with other ostracod specimens recovered from the Needs Camp outcrop.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian (Needs Camp, Lower Quarry). Restriction of this subspecies to this locality suggests that it may have been confined to very shallow (<20 m) normal marine, moderate to high-energy environments with coarse carbonate sand substrates.

Bairdoppilata africana (Chapman, 1916)

Figs 12C–D, 13E–F

Bairdia africana Chapman, 1916: 115, pl. 15, fig. 19a–c. (SAM–2736/19.)

Remarks

The only specimen of this species available is the carapace of the holotype described by Chapman (1916). It has distinctive RV and LV lateral outlines with a strong upward tilt of the RV AM and a tapering outline to the posterior part of the valve. Greatest height occurs at 43 per cent length (cf. 49% in *B. andersoni*) and greatest width (dorsal view) occurs at 50 per cent length (cf. 47% in *B. andersoni*).

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian (Needs Camp, Lower Quarry). Restriction of this species to this locality suggests that it may have been confined to very shallow (<20 m) normal marine, moderate to high energy environments with coarse carbonate sand substrate. Comparable specimens have been recorded from borehole JC-1 (see below).

Bairdoppilata cf. *B. africana* (Chapman, 1916)

Figs 12E-F, 13G-H

Remarks

Specimens of *Bairdoppilata* from the JC-1 borehole are very close to the holotype of *B. africana* from Needs Camp. In particular, they possess the upturned AM outline, and asymmetric DM (maximum height at 40% length) that typifies Chapman's species. The material from borehole JC-1 cannot, however, be unequivocally assigned to *B. africana* because it has a slightly more convex VM outline. Without more topotypic material it is not clear whether this variation falls within the intraspecific morphological range of *B. africana*.

Age, distribution, palaeoecology

Campanian-Maastrichtian in borehole JC-1 (upper and lower limits not known). *B. cf. africana* is the most abundant and widespread ostracod species in this part of the borehole, so presumably it was relatively tolerant of the restricted circulation, high sedimentation rate of the 100-200 m deep delta top basin that the JC-1 Campanian-Maastrichtian sequence is thought to represent.

Bairdoppilata sp. A.

Fig. 14E

Remarks

A distinctive, elongate species with a strongly arched DM. It possesses only a weakly developed typical 'bairdia' boat-shape and has a finely punctate surface ornamentation. No internal views were available and, although this is probably a new species, better preserved material is required to define it.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian Igoda Formation. *B. sp. A* constitutes 6 per cent of the Igoda ostracod population and, as such, is subordinate to *B. andersoni* which constitutes 19 per cent (Table 11). Its restriction to Igoda suggests that it might have been confined to low-energy, normal-marine, moderate-water depths (~100 m, inner shelf).

Genus *Bythocypris* Brady, 1880
Bythocypris richardsbayensis Dingle, 1980
Fig. 14A–C

Bythocypris richardsbayensis Dingle, 1980: 14–16, fig. 6(A–E).

Remarks

Large numbers of well-preserved specimens of this species have been recovered from the outcrops in Zululand north of the Richards Bay borehole, where it consistently constitutes >10 per cent of the total ostracod fauna. In the palaeoecological analyses attempted in the following section, variations in the numbers present of this species are found to be useful indicators in palaeo-sedimentary environmental discrimination and have led to the concept of the 'Bythocypris line' to divide fields on the Cytheracea/Cytherellidae/Bairdiacea + Cypridae (CCBC) triangular diagram (Fig. 68).

Age, distribution, palaeoecology

Santonian II to Maastrichtian III (Richards Bay BH–9 borehole, Monzi, Mfolozi, and Nibela areas in Zululand, Agulhas Bank sample 818, Igoda). *B. richardsbayensis* occurs in ostracod assemblages 1–2, 4a, 4b, 5a, 5b, 6–7, indicating that it had a tolerance of environmental conditions that ranged from high-energy, restricted, shallow marine to quiet, deep, open ocean upper slope. However, Table 4 shows that *B. richardsbayensis* had a definite preference for the deep-water (>500 m, outer shelf/upper slope) environments represented by ostracod assemblages 6–7. Its relationship with *Bairdoppilata* shows some interesting variations (Fig. 10C). In the small number of samples from the shallow-water environments of the Richards Bay BH–9 borehole (Santonian, assemblages 1–2), *Bythocypris richardsbayensis* never constitutes less than 50 per cent of the bairdiacean component, and is frequently the only representative present. This indicates that, although it was at its tolerance limits in these environments, it was far better able to cope with them than *Bairdoppilata*. As soon as deeper-water conditions were established in the Zululand–Richards Bay area in Campanian times, however, the position was immediately reversed, with *Bairdoppilata* constituting less than 40 per cent of the bairdiacean element at only one horizon. In fact, *Bythocypris richardsbayensis* forms >30 per cent of the bairdiacean element only in ostracod assemblage 6. Further examination of Figure 10 indicates that, given the fact that *Bairdoppilata* is always dominant in the deep-water habitats, *Bythocypris* is relatively more tolerant of extremes: shallow, restricted circulation, high energy; and deep, unstable, outer shelf/upper slope, environments.

Bythocypris? sp.
Fig. 14D

Remarks

Six poorly preserved carapaces from borehole JC–1 have tentatively been assigned to *Bythocypris*. Because no internal views are available allocation is

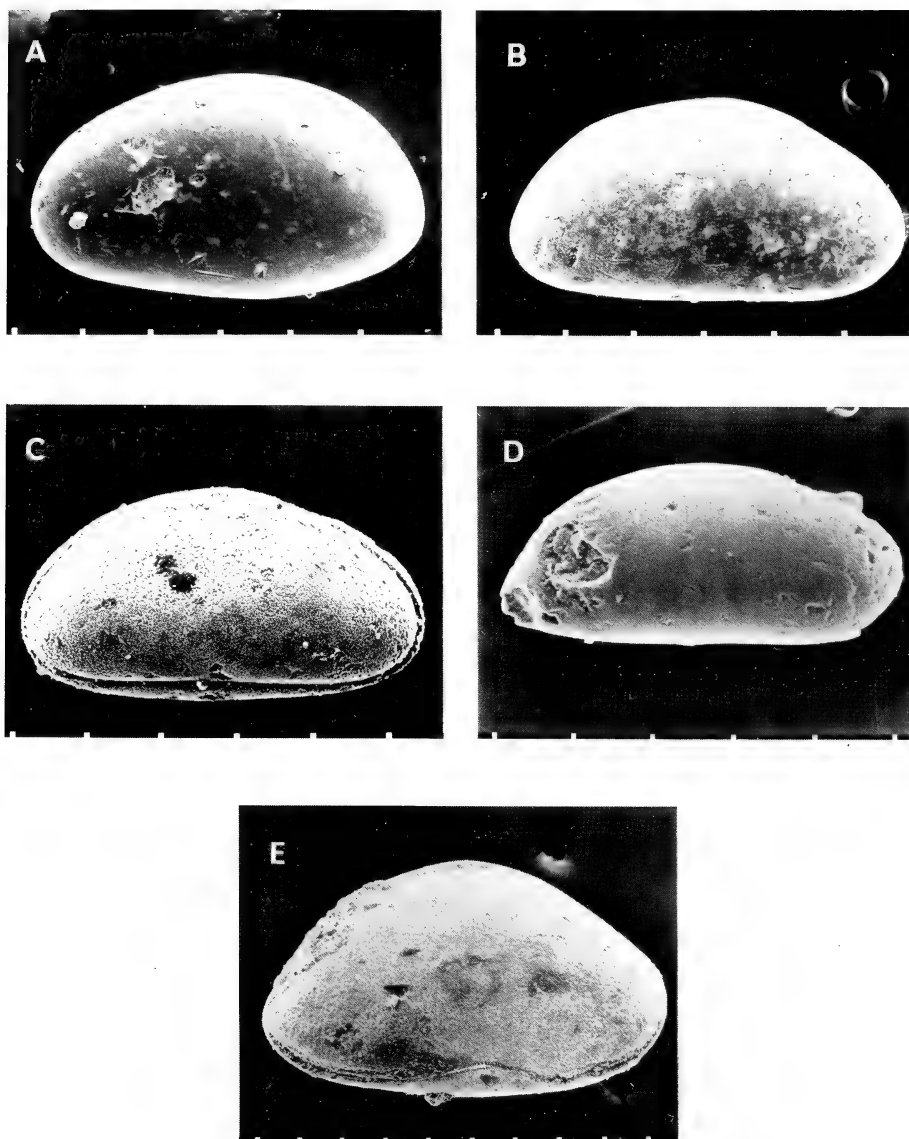


Fig. 14. A–C. *Bythocypris richardsbayensis* Dingle, 1980. A. SAM-K5678, locality 20-1/2, Mfolozi River, LV, Maastrichtian I. B. SAM-K5679, locality 20-1/2, Mfolozi River, RV, Maastrichtian I. C. SAM-K5680, Igoda Formation, Igoda estuary, RV, late Campanian/early Maastrichtian. D. *Bythocypris* sp., SAM-K5681, JC-1 1756 m, RV, Maastrichtian. E. *Bairdoppilata* sp. A, SAM-K5677, Igoda Formation, Igoda estuary, RV, late Campanian/early Maastrichtian.
Scale bars all 100 μ .

purely on external outline, and it is possible that the specimens could belong to *Pontocyprella* or even *Paracypris*. The species differs from *B. richardsbayensis* in having its highest point of outline in the anterior half and in possessing a more asymmetric posterior outline with a more strongly sloping posterodorsal region.

Age, distribution, palaeoecology

Maastrichtian (levels 1 780 m to 1 570 m) in JC-1 borehole. No specimens of this species occur in association with *Inoceramus* prisms in the Campanian-lower Maastrichtian strata, nor at horizons in which charophytes occur. The latter phenomenon suggests that the species was not tolerant of the environments that prevailed during the large influxes of fresh-water debris in the mid-Maastrichtian times.

Superfamily CYPRIDACEA Baird, 1845

The Cypridacea forms a consistent, subsidiary element of the ostracod assemblages in the Upper Cretaceous of south-east Africa, rarely constituting more than 10 per cent. It is represented by two genera (*Paracypris* and *Pontocyprella*) and five species, whose distribution shows strong environmental control (Fig. 15A-C, Table 4). *Paracypris* occurs throughout the Santonian II to Maastrichtian III but is rare above the shallow-water facies of the Santonian, whilst *Pontocyprella* occurs solely in the moderate to deep-water facies of the Upper Campanian and Maastrichtian. The superfamily (*Paracypris* only) has been encountered only occasionally and in trace amounts away from the Zululand-Richards Bay area.

Family **Paracyprididae** Sars, 1923

Genus *Paracypris* Sars, 1866

The genus is present throughout the Campanian-Maastrichtian succession of Zululand, but away from the BH-9 borehole it occurs only as scattered individual valves and carapaces (Fig. 15A) which are invariably poorly preserved. In strata younger than Campanian II it never constitutes more than 2 per cent of the total fauna (Fig. 15C). The two species which were recognized by Dingle (1980) in the well-preserved material of BH-9 borehole (*P. umzambaensis* and *P. zululandensis*) can be recognized in outcrops, but because confident allocation is based on MS pattern, it can rarely be made in these younger strata where good internal views are not available. Consequently, it has not been possible meaningfully to plot the distributions of these two species through the Campanian-Maastrichtian succession in Zululand (for instance in Figs 15, 77-79), and they have been combined under the grouping *Paracypris* spp.

In the other areas, the genus is very rare and poorly preserved: Igoda (11 specimens, *P. umzambaensis*, *P?* sp. A); JC-1 borehole (1 specimen, *P?* sp.); and Agulhas Bank (2 specimens *P. zululandensis*).

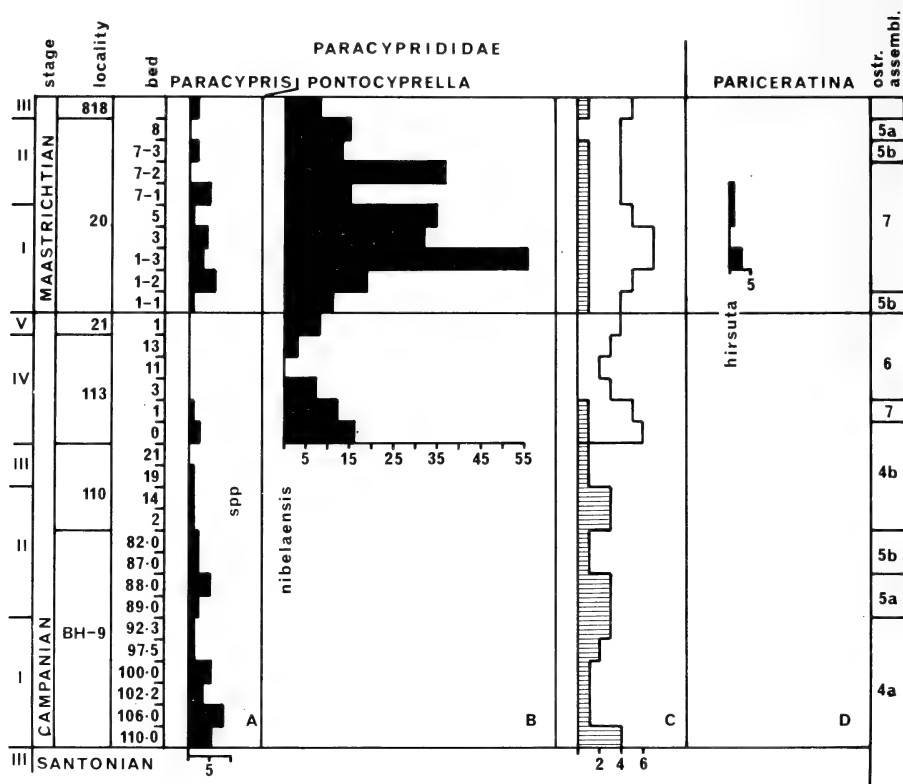


Fig. 15. Distribution of Paracyprididae and *Pariceratina* in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Paracypris* spp. B. Total number of valves of *Pontocyprrella nibelaensis*. C. Percentage of total ostracods: *Paracypris* spp (shaded), *Pontocyprrella nibelaensis* (blank). D. Total number of valves of *Pariceratina hirsuta*.

Paracypris umzambaensis Dingle, 1969

Fig. 16A–C

Macrocypris simplex Chapman, 1898, Chapman, 1904: 233, pl. 29 (fig. 22).

Paracypris? *umzambaensis* Dingle, 1969: 354–356, fig. 5.

Paracypris umzambaensis Dingle, 1980: 17, figs 7A–C, 9A.

Remarks

In the absence of good internal views, differentiation between *P. umzambaensis* and *P. zululandensis* is based on the more acuminate posterior outline of the former. In the case of the plumper varieties of both species, however, differentiation is often subjective, and on the range charts it has not been attempted. Specimens of *P. umzambaensis* from Igoda compare favourably with the plumper varieties from BH-9 borehole (compare Fig. 16A–B), but no internal views were available.

Age, distribution, palaeoecology

Santonian III (Umzamba), Santonian II to Maastrichtian II (BH-9, and Mfolozi River, Zululand), late Campanian/early Maastrichtian (Igoda). The sparse distribution of the genus *Paracypris* in assemblages 5b, 6–7 (Fig. 15C) indicates that it preferred the shallow-water environments of 4a (100–200 m, inner-mid shelf). The meagre evidence available indicates, however, that *P. umzambaensis* was probably more tolerant of the deeper water conditions than was its close relative *P. zululandensis*.

Paracypris zululandensis Dingle, 1980

Fig. 16D

Paracypris zululandensis Dingle, 1980: 17–19, figs 7D–G, 9B.

Remarks

Identifications based solely on valve shape suggest that *P. zululandensis* occurs at outcrops on the Nibela Peninsula, as well as on the Agulhas Bank. As indicated above, however, several identifications in the genus are equivocal, and on the range charts produced herein, no formal attempt has been made to differentiate from *P. umzambaensis*.

Age, distribution, palaeoecology

Santonian II to ?Maastrichtian I (BH-9 borehole and Nibela Peninsula, Zululand), Maastrichtian III (Agulhas Bank). What little data are available suggest that *P. zululandensis* was less able to tolerate the deeper water environments of the Maastrichtian than was *P. umzambaensis*.

Paracypris? sp. A

Fig. 16E

Remarks

An acuminate species, tentatively referred to *Paracypris*, occurs in the Igoda Formation. Preservation is poor and all the specimens are carapaces. The elongate outline is very close to *P. umzambaensis*, but the DM is less strongly arched.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian Igoda Formation at Igoda. This environment is considered to have been low-energy, normal-marine, moderate-water depth (~100 m, inner shelf).

Paracypris? sp.

Remarks

One poorly preserved, fragmentary valve is tentatively referred to *Paracypris* from level 1 835 m (lowermost bed in the Maastrichtian) in the JC-1

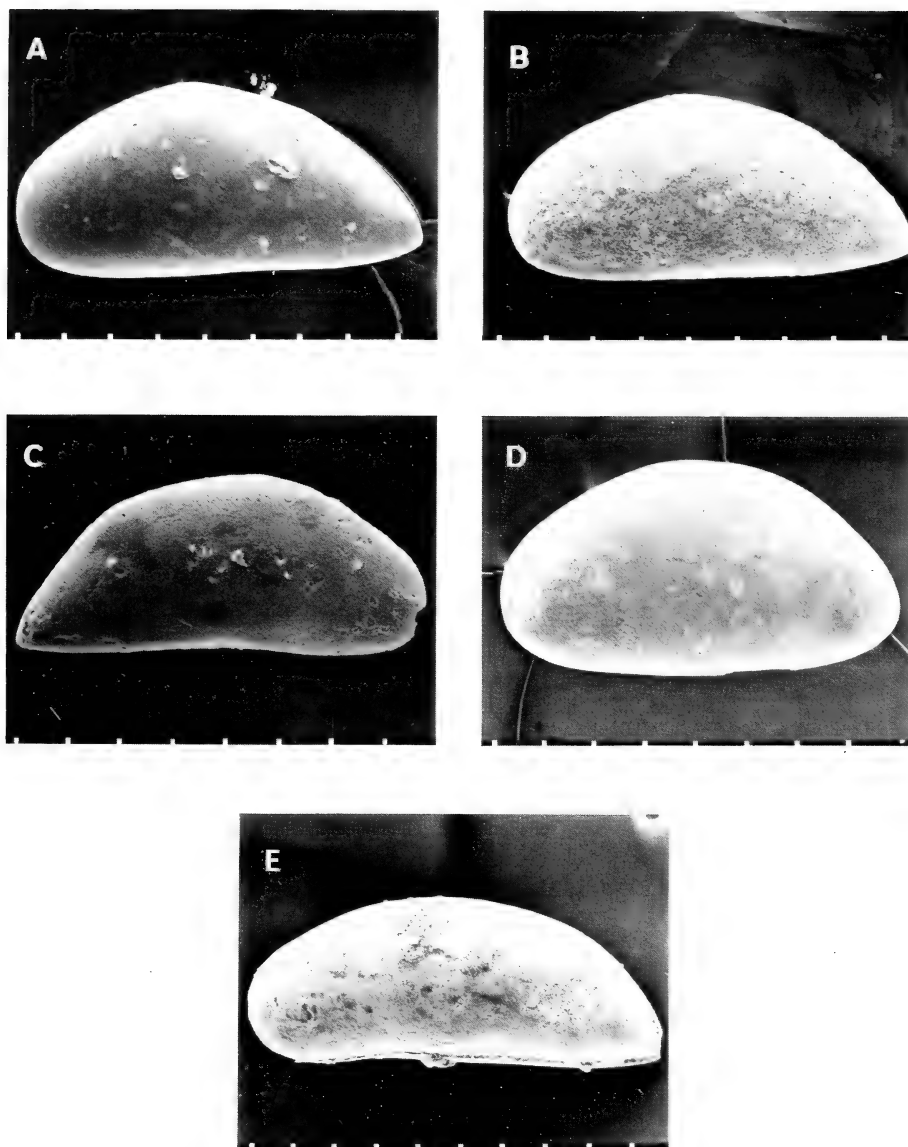


Fig. 16. A-C. *P. umzambaensis* Dingle, 1969. A. SAM-K5586, BH9 88,39 m, LV, Campanian II. B. SAM-K5682, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian. C. SAM-K5683, locality 20-7/1, Mfolozi River, RV, Maastrichtian II. D. *P. zululandensis* Dingle, 1980, SAM-K5590, BH9 110,0 m, LV, Campanian I. E. *P. sp. A*, SAM-K5684, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian. Scale bars all 100 μ .

borehole. Its significance is that it is the only representative of the genus recovered from the Campanian–Maastrichtian section of the JC–1 borehole. Dingle (1976) found small numbers of *Paracypris* (probably a different species) in the Eocene–Oligocene part of the borehole.

Pontocyprrella Lubimova, 1955
Pontocyprrella nibelaensis sp. nov.
Figs 17A–C, 18

Derivation of name

Locality of type.

Holotype

SAM–K5685, RV, locality 113–3, Nibela, Campanian IV

Paratypes

SAM–K5686, LV, locality 113–3, Nibela, Campanian IV

SAM–K5687, RV, locality 113–3, Nibela, Campanian IV

Diagnosis

Large species with prominent anterodorsal margin concavity in RV lateral view.

Description

External features. In lateral view reniform. Asymmetrically rounded AM, broadly pointed PM with apex in ventral region. DM strongly arched with a wide anterodorsal concavity, particularly in RV. VM concave. Greatest height about mid length although the greatest arching of the DM is posterior of this. Valves are plump and large with smooth surfaces.

Internal features. Hinge simple, adont with gently arched groove in RV. MA moderately wide anteriorly, narrow posteriorly and ventrally. Vestibules wide, MPC very short and narrow, at least 20 anteriorly. MS consist of four large oblong scars, two of which are crossed by a small sinus.

Remarks

This large species does not fit comfortably into the genus as erected by Lubimova on *P. harrisiana* (Jones) and has certain characters in common with genera such as *Macrocypis* and *Argilloecia*. However, it lacks the toothed hinge and MS rosette of the former, and the small size and very wide MA of the latter. Our species is very close to ?*Pontocyprrella* sp. described by Neale (1974 pl. 5 (fig. 1)) from the Santonian of western Australia, and has an almost identical MS pattern with *P. dorsoconvexa* Bate from the Campanian of western Australia. The latter species and *P. nibelaensis* differ significantly in lateral outline, however. *Bythocypris simulata* Jones was recorded from the Santonian of

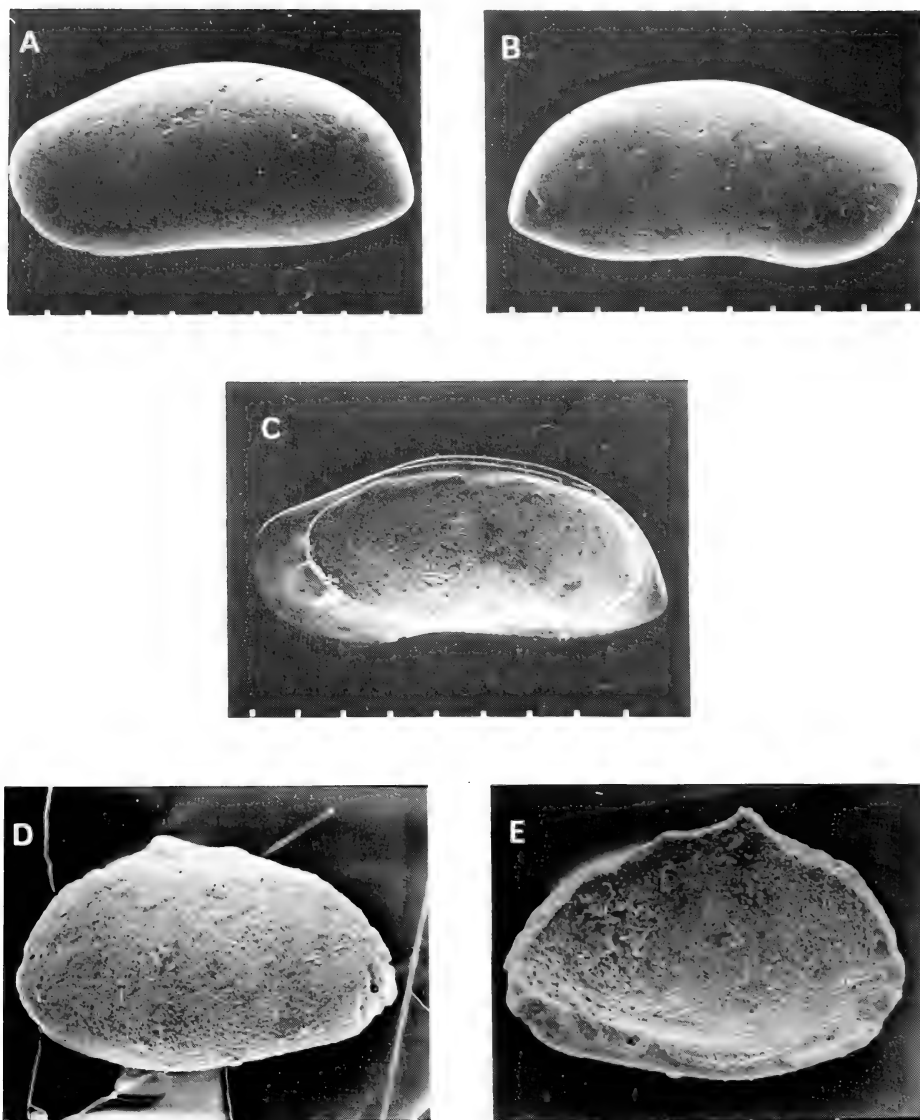


Fig. 17. A-C. *Pontocyprella nibelaensis* sp. nov. locality 113-3, Nibela Peninsula, Campanian IV. A. SAM-K5686, LV. B. Holotype, SAM-K5685, RV. C. SAM-K5687, internal RV. D-E. *Cythere? postcultrata* Chapman, 1916, SAM-2736/18, Lower Quarry Needs Camp, external view (D) and internal view (E).
Scale bars all 100 μ .

Umzamba by Chapman (1904, 1923) and is similar in lateral outline to *P. nibelaensis*, but lacks the anterodorsal concavity.

P. nibelaensis is a characteristic species of the Upper Campanian–Maastrichtian faunas of south-east Africa, locally comprising 9 per cent of the Maastrichtian I ostracod population.



Fig. 18. Muscle scars, *Pontocyprrella nibelaensis* sp. nov., SAM-K5687, locality 113-3, Nibela Peninsula, RV, Campanian IV.
Scale bar 90 μ .

Dimensions (mm)

	length	height
K5685	0,91	0,40
K5686	0,94	0,44
K5687	0,87	0,38

Age, distribution, palaeoecology

Campanian IV to Maastrichtian III (Nibela and Monzi areas of Zululand, and Agulhas Bank). *P. nibelaensis* occurs in ostracod assemblages 4b, 5a, 5b, 6-7 (Fig. 15B), and seems to have preferred quiet, deep-water environments (>500 m, outer shelf/upper continental slope).

Superfamily CYTHERACEA Baird, 1850

The numerical importance of the Cytheracea within the Campanian–Maastrichtian ostracod populations of south-east Africa (as monitored in Zululand) is directly controlled by changes in palaeosedimentary environments in time and space: in the shallower water environments the superfamily constitutes between 40 and 60 per cent, whereas in deeper-water environments this figure drops to between 20 and 30 per cent. Thus, on Figure 67 there is a sharp decline in the cytheracean percentage (50% to 20%) just above the Campanian I–II boundary in the Richards Bay BH-9 borehole, and a similarly dramatic decline (40% to 20%) in the lower part of Campanian IV at outcrops to the north in Zululand. As will be explained in a later section, these changes are mirrored in other facets

of the overall ostracod populations, and occur at different times in different localities because of the strongly diachronous nature of the facies changes in south Zululand.

At the other localities in south-east Africa from which either small numbers of samples or only small ostracod populations are available, the importance of the superfamily varies considerably: Igoda and Needs Camp (late Campanian/early Maastrichtian) 57% and 6%, respectively; sample 818 Agulhas Bank (Maastrichtian III) 83%; and in the Campanian–Maastrichtian section of the JC–1 borehole 26% (11% *Krithe* and 15% ornamented species). In these areas it has not been possible satisfactorily to monitor the temporal distribution of the superfamily, but in the discussion section the significance of particular elements of the cytheracean component are commented upon where a comparison with the Zululand faunas is thought feasible.

In terms of number of cytheracean species as percentage of total number of extant species, the superfamily is dominant, even in the sedimentary environments where it is numerically not important (see Table 16). There is a slight decline from 67 per cent of total species in the Campanian I–II to 64 per cent in the Campanian IV, followed by a sharp increase to a high of 72 per cent in the Maastrichtian I. Thereafter, this diversity declines to 60 per cent in the Maastrichtian II. The Igoda populations follow the regional trend at 71 per cent in the late Campanian/early Maastrichtian.

Family *Cytheridae* Baird, 1850

Genus *Cythere* Mueller, 1785

Cythere? *postcultrata* Chapman, 1916

Fig. 17D–E

Cythere postcultrata Chapman, 1916: 116, pl. 15 (figs 18a–b). (SAM–2736/18.)

Remarks

The holotype of this species (SAM–2736/18) is a poorly preserved fragment of indeterminate taxonomic status, which almost certainly does not belong to genus *Cythere*. In his description, Chapman (1916) considered the specimen to be a left valve with the ‘keel shaped prominence’ lying along the ventral margin, but if the fragment is from an ostracod, then this orientation seems unlikely and it is suggested that it may be a left valve from which the dorsal and posterior areas have removed. Internal views show no evidence of MS, recognizable MA features, or hingement, though if the suggestion here on orientation is correct then the hinge has been broken off.

Chapman assigned no other specimens to this species and in our material nothing, with the possible exception of *Pondoina*, looks at all like it.

It is possible that the holotype is not even a fragment of an ostracod and it is certainly not suitable to be designated as a holotype. This presumably invalidates its taxonomic assignment by Chapman although we have not formally applied to have the name suppressed.

Family **Bythocytheridae** Sars, 1926
Genus *Pariceratina* Gründel & Kozur, 1971

Pariceratina hirsuta sp. nov.

Fig. 19A–D

Derivation of name

Latin *hirsuta* (rough, uneven): reference to rough valve surface.

Holotype

SAM-K5688, RV, locality 20–1/3, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5689, LV, locality 20–7/1, Mfolozi River, Maastrichtian II

SAM-K5690, LV, locality 20–1/3, Mfolozi River, Maastrichtian I

Diagnosis

Species with rough surface ornamentation of small spines, and an upturned caudal process.

Description

External features. In lateral view AM rounded and spinose, PM acuminate with an upturned caudal process. VM slightly convex, DM undulating. Surface ornamented with three large ventral spines distributed equidistantly along VM. Surface ornamented all over with fine reticulation and small conjunctive and disjunctive spines. The large surface spines bear small secondary spines.

Internal features. The hinge is rudimentary, consisting of a smooth LV bar and corresponding RV groove, but also has very small smooth terminal ridges in the RV. Inner surface of valve has large sulci leading to the three large lateral spines. MS consist of a curved row of six oblong adductor scars and one rounded anterior scar. No clear views of MA available.

Remarks

P. hirsuta differs from the closely related Australian species *P. trispinosa* (Neale, 1975) in being less spinose marginally, having an upturned caudal process, and in lacking ridges on its ventral surface.

Dimensions (mm)

	length	height
K5688	0,68	0,35
K5689	0,55	0,30
K5690	0,55	0,31
Other material	0,60	?

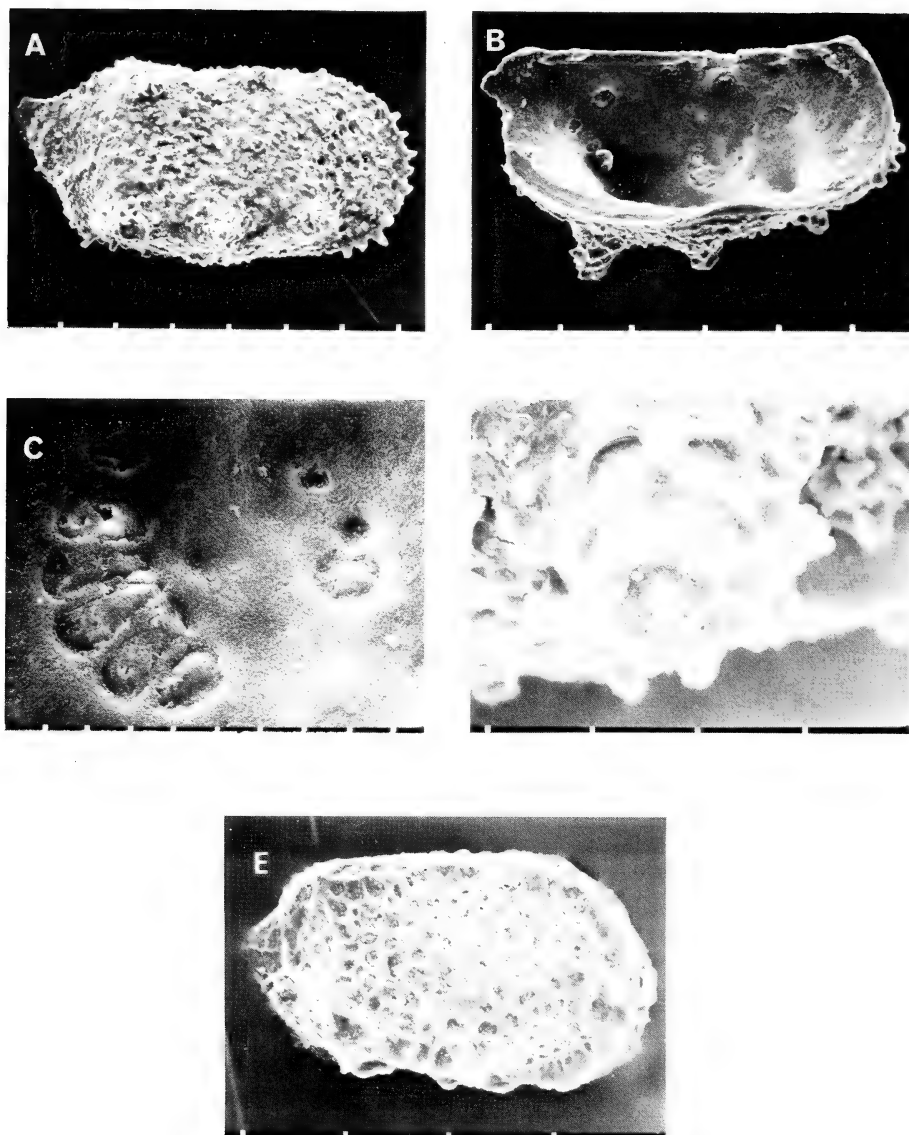


Fig. 19. A-D. *Pariceratina hirsuta* sp. nov. A. Holotype, SAM-K5688, locality 20-1/3, Mfolozi River, RV, Maastrichtian I. B. SAM-K5689, locality 20-7/1, Mfolozi River, internal LV, Maastrichtian II. C. SAM-K5689, locality 20-7/1, Mfolozi River, MS LV, Maastrichtian II. D. SAM-K5690, locality 20-1/3, Mfolozi River, detail posteroventral spine LV, Maastrichtian I. E. *Eucytherura? pyramidatus* sp. nov., holotype, SAM-K5691, locality 21-1, Monzi, RV, Campanian V.

Scale bars: C = 10 μ , D = 30 μ , others = 100 μ .

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *P. hirsuta* is confined to ostracod assemblage 7 of which it is a minor member. This suggests that it was environmentally bound by deep, oceanographically stable conditions (>500 m, outer shelf/upper continental slope) (Fig. 15D).

Family **Cytheruridae** Müller, 1894

A family that is present only in the deeper water environments of the upper Campanian and Maastrichtian in Zululand (Fig. 22). It is represented by three genera and four species, only one of which (*Pedicythere fragilis*) attains any numerical importance (up to 13% of the cytheracean population).

Genus *Eucytherura* Müller, 1894*Eucytherura?* ***pyramidatus*** sp. nov.

Fig. 19E

Derivation of name

Latin *pyramidatus* (pyramidal): reference to pyramid-shaped posteroventral process.

Holotype

SAM-K5691, carapace, locality 21-1, Monzi, Campanian V.

Diagnosis

Species with pyramid-shaped posteroventral process that is joined to a posterodorsal process by a vertical ridge.

Description

External features. In lateral view, quadrate with broadly rounded AM, acuminate PM with caudal process. DM and VM straight. Flared ventrolateral ridge runs from anterior quarter to a pyramid-shaped posteroventral process at three-quarters length. A similar-shaped, less conspicuous process lies in a posterodorsal location at the end of a short and poorly defined dorsal rib. The two processes are connected by a vertical rib. There is a prominent AM rim with a lipped indentation at about mid height. Valve surface reticulate, fossae being larger adjacent to the main ribs. Eye spot prominent at anterior cardinal angle.

Internal features. No internal features seen.

Remarks

Generic assignment is uncertain because no internal features were seen, though valve outline and geometry are typical for the genus. The posteroventral process is reminiscent of the icositetrahedron-shaped process of *E. antipodum* from the Santonian of western Australia (Neale 1975), but the African species differs by lacking an anterodorsal process and curved posterodorsal rib.

Age, distribution, palaeoecology

Campanian V (Monzi, Zululand). The one carapace available occurred in ostracod assemblage 6 which represents a deep-water (>500 m, outer shelf/upper continental slope), oceanographically unstable environment (Fig. 22A).

Dimensions (mm)

	length	height
K5691	0,40	0,23

Genus *Cytheropteron* Sars, 1866

Cytheropteron brenneri sp. nov.

Fig. 20A

Derivation of name

Named after Dr P. Brenner for his contribution to the knowledge of South African lower Cretaceous ostracods.

Holotype

SAM-K5692, RV, locality 20-5, Mfolozi River, Maastrichtian I.

Diagnosis

Elongate species with pointed, spinose alae.

Description

External features. RV elongate with narrowly rounded AM and upturned caudal process. DM broadly arched with a broad step at anterior cardinal angle. VM straight. There is a large, pointed ala which bears spines along its posterior edge and has a mucrose terminal spine. The ala protrudes almost at right angles from the valve surface and is smooth distally and finely punctate proximally. The rest of the lateral surface is smooth.

Internal features. Not clearly seen, except anterior MA is wide, with a small central vestibule and possibly 10-12 short, faint MPC. Posterior MA is small, but MPC could not be studied.

Remarks

C. brenneri is similar to *C. (Aversovalva) mcomborum* Neale, 1975, but the latter has an overall pitted surface, posteriorly deflected alae, and a more symmetrically acuminate PM. *C. (A.) mcomborum* is from the Santonian of western Australia.

C. brenneri is a minor species that never exceeds 1 per cent of the Cytheracean population.

Dimensions (mm)

	length	height (over ala)
K5692	0,40	0,28

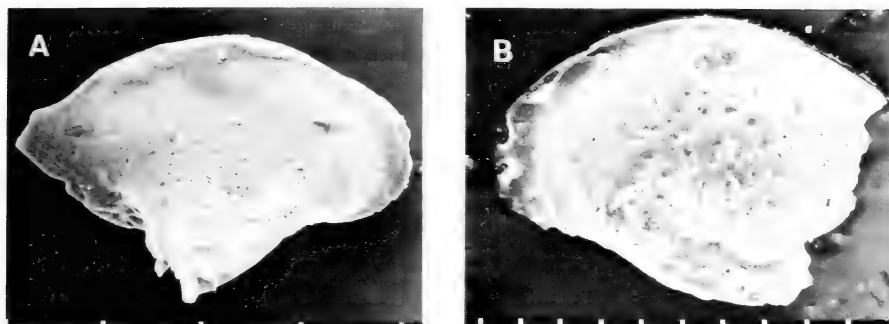


Fig. 20. *Cytheropteron*. A. *C. brenneri* sp. nov., holotype, SAM-K5692, locality 20-5, Mfolozi River, RV, Maastrichtian I. B. *C. cf. C. westaustraliense* Neale, 1975, SAM-K5693, locality 20-5, Mfolozi River, LV, Maastrichtian I.
Scale bars: A = 100 μ , B = 30 μ .

Age, distribution, palaeoecology

Late Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *C. brenneri* occurs in ostracod assemblages 5a, 5b, and 7 (Fig. 22B). Because of the small numbers found, it is not possible confidently to predict which sedimentary environment it preferred; it is known to have inhabited environments ranging from quiet-water, moderate depth (?200–300 m, mid-outer shelf) to quiet, deep water (>500 m outer shelf/upper continental slope).

Cytheropteron cf. *C. westaustraliense* Neale, 1975

Fig. 20B

Cytheropteron (*Aversovalva*) *westaustraliense* Neale, 1975: 27–30, pl. 13 (fig. 5–7), text fig. 4c–d, g–h.

Remarks

One valve which is very similar to Neale's original description, notably the thick rimmed, dorsally pitted alae. The African form differs slightly in having a more arched DM in LV and subtly more posteriorly deflected alae, and these differences may reflect a new species. Whatever the case, the two types are very closely related, though they show a significant age difference: Santonian in the Gingin chalk of Western Australia, and Maastrichtian I in the St Lucia Formation.

Dimensions (mm)

	length	height (over ala)
K5693	0,30	0,20

Age, distribution, palaeoecology

Maastrichtian II (Mfolozi River, Zululand). The one valve available was found in ostracod assemblage 7 (Fig. 22C), which represents a deep-water (>500 m, outer shelf/upper continental slope) oceanographically stable environment.

Genus *Pedicythere* Eagar, 1965

Pedicythere fragilis sp. nov.

Figs 21A–F, 23A–B

Derivation of name

Latin *fragilis* (fragile); reference to delicate nature of valves.

Holotype

SAM-K5694, RV, locality 20–7/3, Mfolozi River, Maastrichtian II

Paratypes

SAM-K5695, LV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5696, RV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5697, RV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5698, LV, locality 20–1/2, Mfolozi River, Maastrichtian I

Diagnosis

Small, thin-shelled, acutely alate species with frilled AM and long, posteroventral spines.

Description

External features. In lateral view, AM asymmetric, frilled, somewhat ragged in appearance, PM with posterodorsal caudal process and three ventrally curved, tusk-like posteroventral spines. DM straight, inflected upwards at posterior extremity. VM convex, but hidden in lateral view. Surface features dominated by massive, hollow, pointed alae, the leading edges of which continue as narrow ridges to the AM. In dorsal view, the distal ends of the alae project almost as far back as the PM, and in ventral view the alae bear three short longitudinal ribs. Valve surface smooth, with rare puncta.

Internal features. MA and MS not seen clearly. Hinge modified amphidont: in RV, ATE is a subdivided peg, PTE is elongate and denticulate; in LV, ME is a dentate bar, and the ATE socket is open to the body of the valve ventrally (a feature noted by Neale (1975) in his Australian species *P. australis*).

Remarks

P. fragilis resembles *P. australis* Neale, 1975, from the Santonian of Western Australia, but differs in having more prominent alae and a frilled AM. It has a prominent posterodorsal caudal process like *P. sp.* recorded by Bate (1972) from the Campanian of Western Australia, but differs in ala shape.

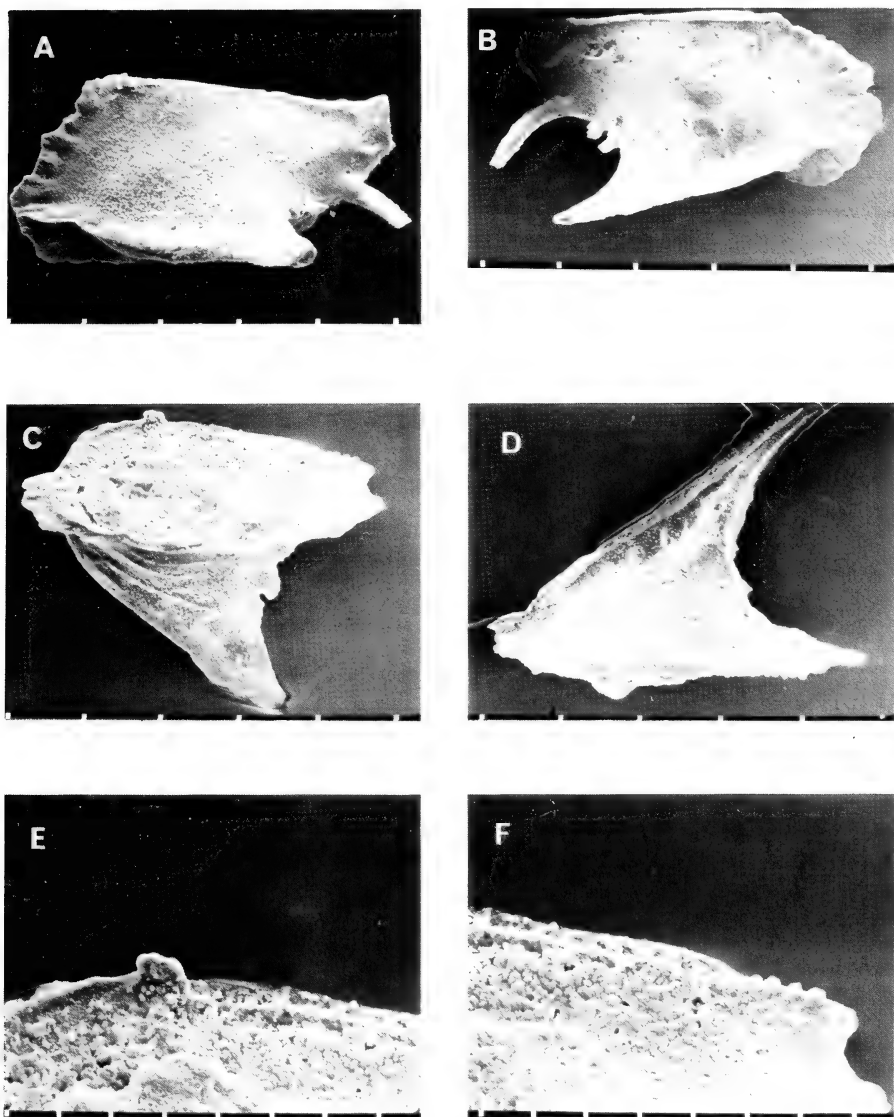


Fig. 21. *Pedicythere fragilis* sp. nov. A. SAM-K5695, locality 20-1/2, Mfolozi River, LV, Maastrichtian I. B. Holotype, SAM-K5694, locality 20-7/3, Mfolozi River, RV, Maastrichtian II. C. SAM-K5696, locality 20-1/2, Mfolozi River, internal RV, Maastrichtian I. D. SAM-K5697, locality 20-1/2, Mfolozi River, dorsal view RV, Maastrichtian I. E-F. SAM-K5696, locality 20-1/2, Mfolozi River, detail hinge ATE(E) and PTE(F), Maastrichtian I. Scale bars: E-F = 30μ , others = 100μ .

Dimensions (mm)

	length (excl. spines)	height (over ala)	width (over ala)
K5694	0,46	0,27	
K5695	0,45	0,22	
K5696	0,45	?	
K5697	0,45		0,33
K5698	0,41	?	
Other material	0,40	0,25	
Other material	0,40	0,25	

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *P. fragilis* is found in ostracod assemblages 5a, 5b, and 7 (Fig. 22D), and although it constitutes between 1 per cent and 13 per cent of the Cytheracea population, its distribution does not allow a definitive statement on its environmental preferences. It appears to have preferred 5a: quiet, open-water, moderate-depth (?200–300 m, mid-outer shelf) conditions, but clearly could tolerate greater depths.

Family **Schizocytheridae** Mandelstam, 1960

Bate (1972) grouped the following genera into the subfamily Schizocytherinae Mandelstam, 1960: *Schizocythere*, *Cnestocythere*, *Acrocythere*, *Amphicytherura*, *Apateloschizocythere*, and *Sondagella*. Subdivision is based upon presence and/or absence of eyes, the possession of schizodont or antimerodont hinges, and differences in valve outline and ornamentation. Present data show that four of these genera can be recognized in the South African Lower (*Sondagella* and *Acrocythere*) and Upper Cretaceous (*Amphicytherura* and *Apateloschizocythere*).

Together with the Brachyocytheridae, the Schizocytheridae rank second in importance behind the Tachyleberididae in diversity (6–18%) and consistent distribution within the cytheracean families of the south-east African Campanian–Maastrichtian strata (Table 17). It is represented by two genera and six species which consistently constitute between 5 and 10 per cent of the Cytheracea population, but locally makes up more than 10 per cent (Fig. 22K).

Genus *Amphicytherura* Butler & Jones, 1957

This genus ranges throughout the Santonian–Maastrichtian rocks of south-east Africa, and in the Campanian–Maastrichtian section is represented by four species: *A. tumida*, *A. zululandensis*, *A. sp. A*, and *A. armatus*. All four species occur in the Campanian, but only two persist into the Maastrichtian (Fig. 22E–H).

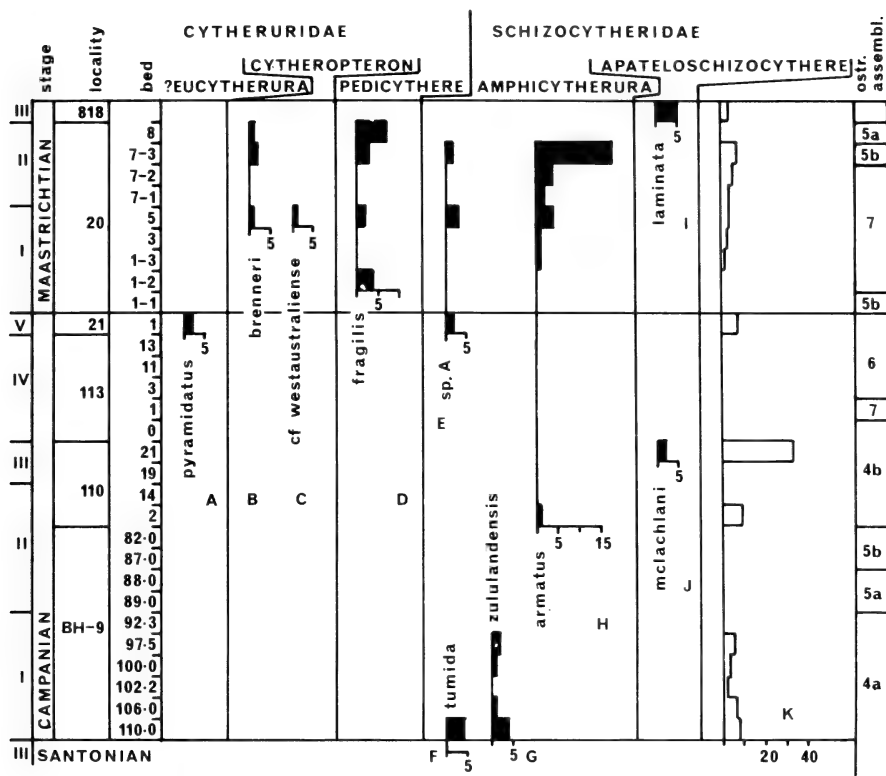


Fig. 22. Distribution of Cytheruridae and Schizocytheridae in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Eucytherura? pyramidatus*. B. Total number of valves of *Cytheropteron brenneri*. C. Total number of valves of *Cytheropteron* cf. *C. westaustraliense*. D. Total number of valves of *Pedicythere fragilis*. E. Total number of valves of *Amphicytherura* sp. A. F. Total number of valves of *Amphicytherura tumida*. G. Total number of valves of *Amphicytherura zululandensis*. H. Total number of valves of *Amphicytherura armatus*. I. Total number of valves of *Apateloschizocythere laminata*. J. Total number of valves of *Apateloschizocythere mclachlani*. K. Schizocytheridae as percentage of Cytheracea.

Amphicytherura tumida Dingle, 1969

Figs 23C, 25A

Amphicytherura (A.) *tumida* Dingle, 1969: 368–370, fig. 13.

Amphicytherura tumida Dingle, 1980: 20–21, fig. 10A–F.

Remarks

No further specimens of this species have been found above the top levels from which it was recorded in the Richards Bay borehole (bed number 110.0) (Dingle 1980) where it is evidently at the top of its range. One carapace has been found in sample Pi13 (Campanian I) at Umzamba. Locally, therefore, the extinction of *A. tumida* can be used as a rough guide to the Santonian–Campanian boundary.

Age, distribution, palaeoecology

?Santonian II to Campanian I (Umzamba), early Santonian III to earliest Campanian I (Richards Bay BH-9 borehole). *A. tumida* has been found in ostracod assemblages 2, 2/3 transition, and 4a, indicating that it was moderately environmentally tolerant, but preferred the shallow-water (<100 m, inner shelf) low-energy, restricted circulation environments of assemblage 2 (Table 4).

Amphicytherura zululandensis Dingle, 1980

Figs 23D, 25B

Amphicytherura zululandensis Dingle, 1980: 21–24, fig. 11A–G*Remarks*

This distinctive species has not been found outside the Richards Bay BH-9 borehole.

Age, distribution, palaeoecology

Campanian I (Richards Bay BH-9 borehole). *A. zululandensis* is confined to assemblage 4a and was environmentally bound by quiet, moderate depths (?100–200 m inner-mid shelf), where it seems to have replaced *A. tumida* and locally constitutes between 5 per cent and 10 per cent of the cytheracean fauna (Fig. 22G, K, Table 4).

Amphicytherura sp. A

Fig. 23E

Remarks

Seven specimens of a species that is close to *A. tumida* have been found at three levels in upper Campanian–Maastrichtian outcrops in Zululand. They are poorly preserved but probably represent a new species which differs from *A. tumida* on the following points: sp. A has a more symmetric PM outline and lacks the typical posteroventral cutaway of *A. tumida*; the DM and VM of sp. A are almost parallel, giving it a more rectangular outline than *A. tumida*; in the LV hinge, the PTE of *A. tumida* is larger and more complex and the anterior end of the ME is oblong, the latter is shorter and peg-like in sp. A.

Age, distribution, palaeoecology

Campanian V to Maastrichtian II (Monzi and Mfolozi River, Zululand) (Fig. 22E). *A. sp. A* is found in ostracod assemblages 5b, 6–7, though with the small numbers involved it is not possible to say which it preferred. Presumably it was restricted to water depths >300 m, i.e. it inhabited outer-shelf and upper-slope environments (Table 4).

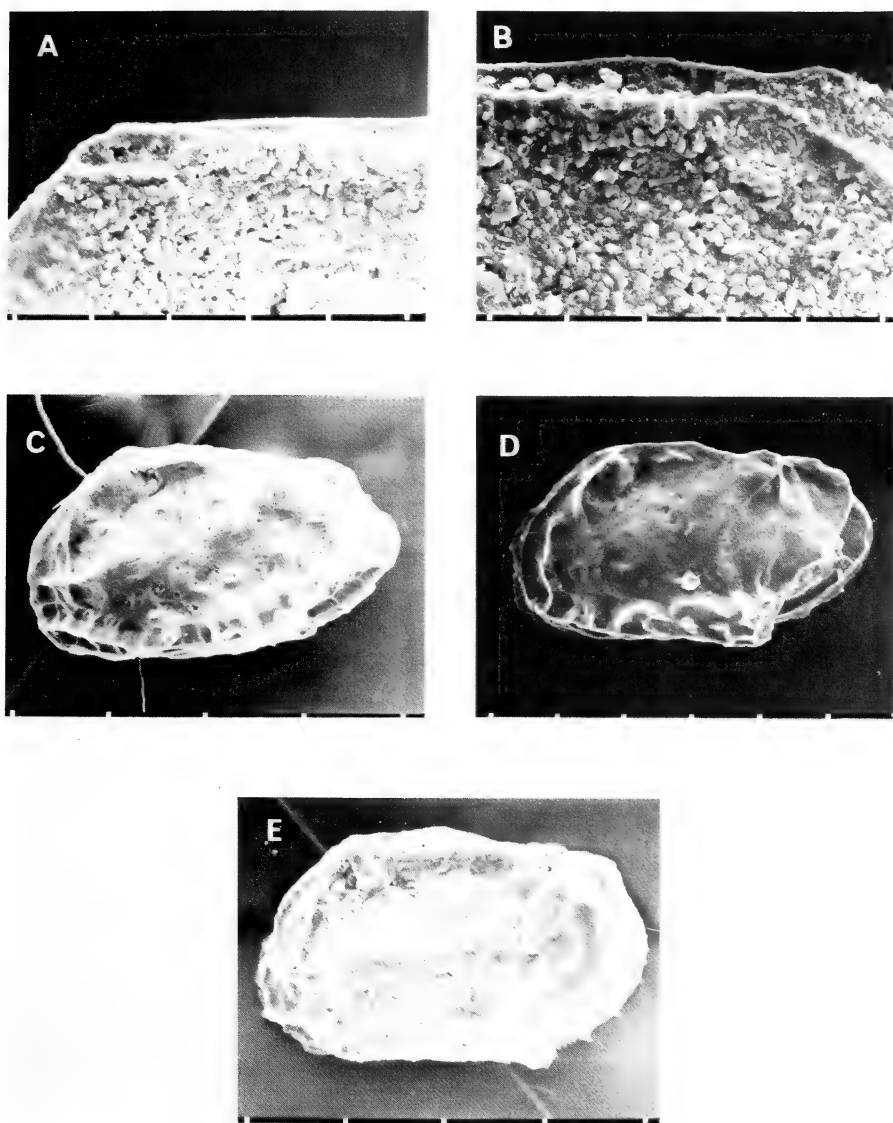


Fig. 23. A-B. *Pedicythere fragilis* sp. nov., SAM-K5698, locality 20-1/2, Mfolozi River, internal LV PTE(A) and ATE(B), Maastrichtian I. C-E. *Amficytherura*. C. *A. tumida* Dingle, 1969, SAM-K5699, BH9 110,0 m, LV, Campanian I. D. *A. zululandensis* Dingle, 1980, SAM-K5599, BH9 97,5 m, LV, Campanian I. E. *A. sp.* A, SAM-K5700, locality 21-1, Monzi, LV, Campanian V.

Scale bars: A-B = 30 μ , others = 100 μ .

Amphicytherura armatus sp. nov.

Figs 24A–E, 25C

Derivation of name

Latin *armatus* (armoured): reference to encased or armoured appearance.

Holotype

SAM-K5701, LV, locality 20–3, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5702, RV, locality 20–7/3, Mfolozi River, Maastrichtian II

SAM-K5703, LV, locality 20–7/3, Mfolozi River, Maastrichtian II

SAM-K5704, RV, locality 20–7/3, Mfolozi River, Maastrichtian II

Diagnosis

Heavily calcified species with a curved posterodorsal flange-like protrusion.

Description

External features. In lateral view, AM asymmetrically rounded with frilled edge, PM acuminate, slightly asymmetric. DM and VM almost straight and nearly parallel. Surface ornamented with irregular pits, indistinct nodes, plate-shaped swellings and fine ribs, giving a fanciful appearance of a suit of armour. A wide swelling runs to the posterodorsal corner from the indistinct SCT, and a narrow ridge runs anteriorly to the AM. There is a prominent posterodorsal shoulder which in well-preserved specimens is delicately ridged and perforate. Behind this lies a curved flange which projects above the dorsal margin and hides the posterodorsal outline. There is a keel-like ventrolateral ridge that runs from the AM to a stubby, wing-like posteroventral corner. The proximal surface of this keel has coarse quadrate reticulation. Eye spot is a prominent dome.

Internal features. Hinge schizodont, with anterior tooth of LV ME trifid, ATE RV bifid, and PTE RV coarsely dentate. ME is denticulate. MA moderately wide, possibly with very narrow vestibules anteriorly. Up to ten straight, widely spaced anterior MPC; up to six straight, widely spaced posterior MPC. MS: an oval anterior scar and curved row of four large, ovate adductors, the second of which is wedge-shaped.

Remarks

A. armatus bears a resemblance to *A. tumida*, but differs in being less elongate, in having a subtly different lateral surface morphology, especially in the shape of the posterodorsal and posteroventral swellings, and in possessing the curved posterodorsal flange. The hinges of the two species also differ: the anterior tooth of LV ME in *A. tumida* is bifid, and the ATE of *A. tumida* is more coarsely dentate. The MS also differ slightly (Fig. 25).

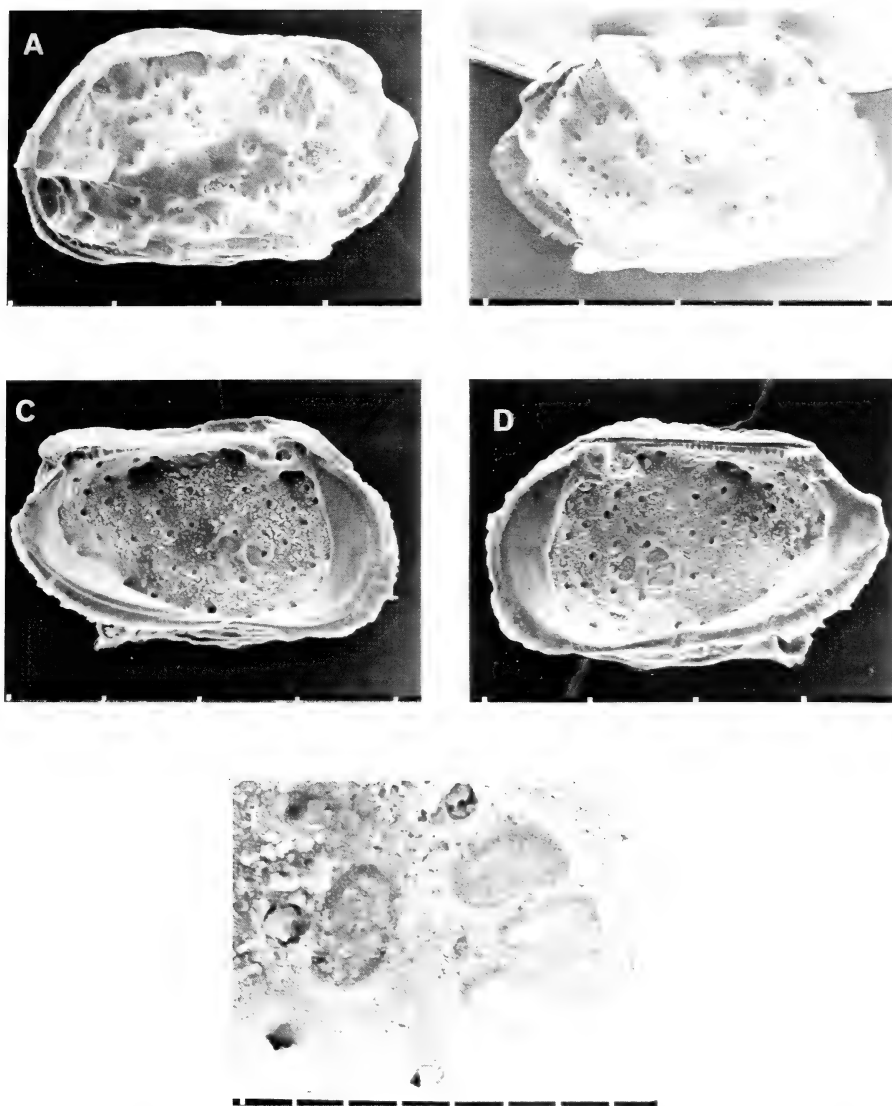


Fig. 24. *Amphicytherura armatus* sp. nov. A. Holotype, SAM-K5701, locality 20-3, Mfolozi River, LV, Maastrichtian I. B. SAM-K5702, locality 20-7/3, Mfolozi River, RV, Maastrichtian II. C. SAM-K5703, locality 20-7/3, Mfolozi River, internal LV, Maastrichtian II. D-E. SAM-K5704, locality 20-7/3, internal RV(D), MS(E), Maastrichtian II. Scale bars: E = 10μ , others = 100μ .

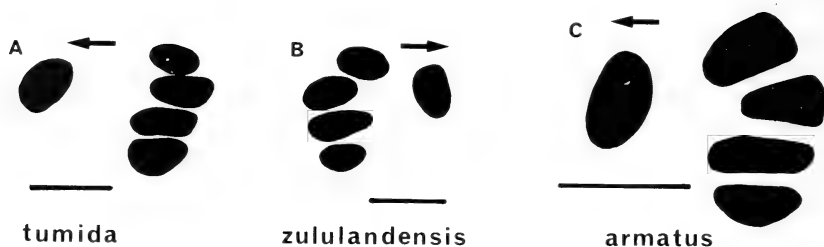


Fig. 25. Muscle scars of *Amphicytherura*. A. *A. tumida* Dingle, 1969, Umzamba cliff, RV, Santonian. B. *A. zululandensis* Dingle, 1980, SAM-K5601, BH9 110,0 m, LV, Campanian I. C. *A. armatus* sp. nov., SAM-K5704, locality 20-7/3, Mfolozi River, RV, Maastrichtian II. Scale bars 30 μ .

Dimensions (mm)

	length	height
K5701	0,38	0,22
K5702	0,40	0,25
K5703	0,40	0,24
K5704	0,38	0,24
Other material	0,40	0,24
Other material	0,36	0,24
Other material	0,45	0,26

Age, distribution, palaeoecology

Campanian II to Maastrichtian II (Nibela and Mfolozi River, Zululand)—all records, except one specimen from locality 110 on the Nibela Peninsula, are from Maastrichtian I–II of the Mfolozi River section (locality 20) (Fig. 22H). *A. armatus* occurs in ostracod assemblages 4b, 5b, and 7, but is consistent, and in relatively large numbers (*for the family*) only in 5b and 7. It is not possible to say precisely where its preference lay, but apparently it was most successful in deep water (?300–>500 m outer shelf to upper slope) (Table 4).

Genus *Apateloschizocythere* Bate, 1972

Apateloschizocythere mclachlani sp. nov.

Fig. 26A–B

Derivation of name

Named after Dr I. McLachlan for his contribution to the knowledge of South African Mesozoic stratigraphy.

Holotype

SAM-K5705, Carapace, locality 110–21, Nibela, Campanian III.

Diagnosis

Species with distinct caudal process and four lateral ridges emanating from the AM.

Description

External features. In lateral view, small quadrate species with rounded AM and symmetrical, acuminate PM with a caudal process. DM and VM straight. Cardinal angles clearly defined. Surface strongly reticulate with horizontal and vertical blade-like muri. Four longitudinal ridges emanate from the AM: a ventral one which defines the ventrolateral outline; a lateroventral ridge which is deflected ventrally in the posterior half and which ends in a sharp wing-like process; a median ridge which deflects ventrally just in front of mid length; and a short ridge above mid height which has a sharp ventral offset in a subcentral position and extends to about three-quarters length. Dorsal part of valve dominated by short vertical ridges and weaker longitudinal muri.

Internal features. Not seen.

Remarks

A. mclachlani differs from the genotype (*A. geniculata* Bate, 1972) by possessing a caudal process and a fourth lateral ridge. In Australia, *A. geniculata* ranges from Santonian to Campanian. *A. laminata* (Maastrichtian, Agulhas Bank) has a very similar rib pattern to *A. mclachlani*, but has a prominent LV anterodorsal ear and delicate secondary reticulation.

Dimensions (mm)

	length	height
K5705	0,39	0,24

Age, distribution, palaeoecology

Campanian III (Nibela Peninsula, Zululand). *A. mclachlani* has been found only in ostracod assemblage 4b, indicating that it was bound to moderate-depth (?200 m inner-mid shelf) environments (Fig. 22J).

Apateloschizocythere laminata (Dingle, 1971)

Fig. 26C–F

Acrocythere? laminata Dingle 1971: 403–404, fig. 6.

Remarks

The uncertainty of generic assignment for this species when it was erected was resolved by the creation of *Apateloschizocythere* by Bate (1972). SEM photographs included herein supplement the original description and indicate that the ornamentation of *A. laminata* consists of a coarse first-order frame with prominent blade-like longitudinal ridges and vertical muri, and a lace-like secondary reticulation. Although Dingle (1971) indicated 'indistinct eyespots', the species is now known to be blind.

A. laminata has a similar first-order surface ornamentation to the genotype *A. geniculata* Bate (1972), and both species possess sieve plates over the normal pore canal apertures with hair pore openings (Fig. 26E). The MS of *A. laminata*

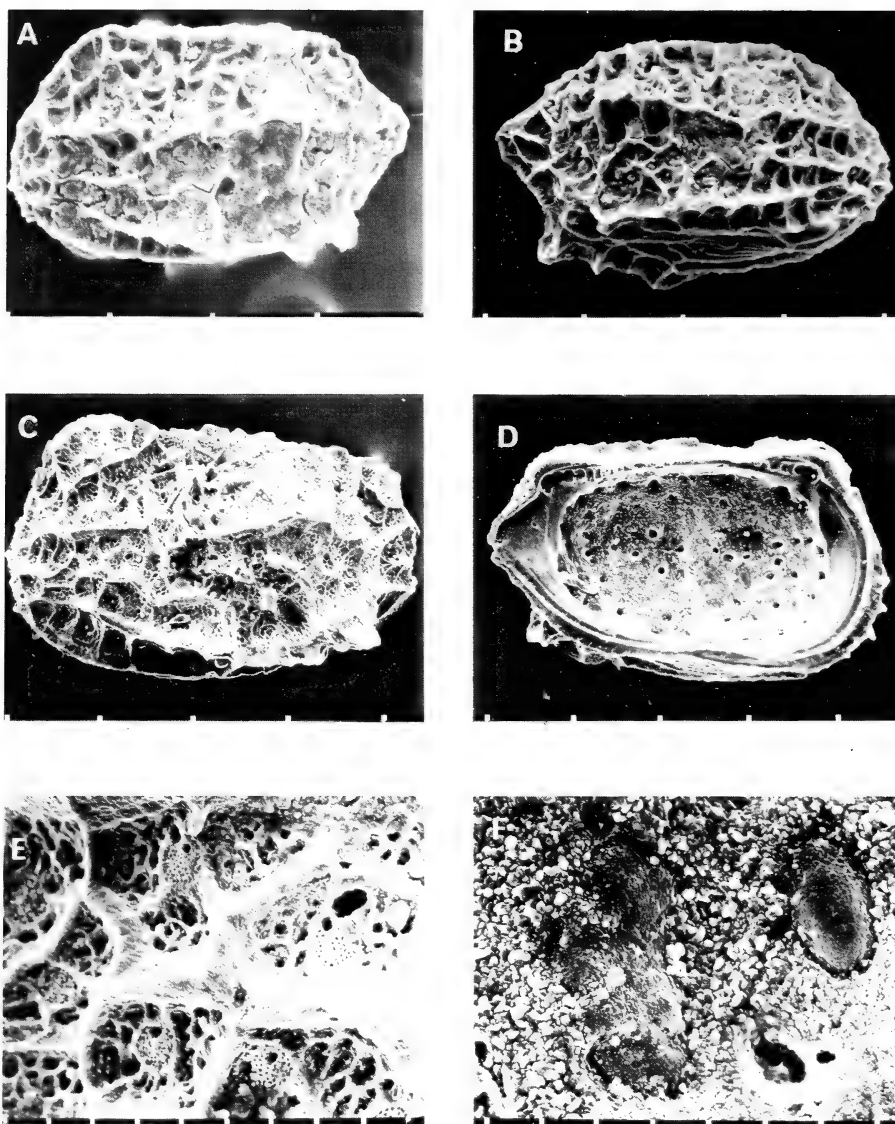


Fig. 26. *Apateloschizocythere*. A-B. *A. mclachlani* sp. nov., holotype, SAM-K5705, locality 110-21, Nibela Peninsula, LV(A) and RV(B), Campanian III. C-F. *A. laminata* (Dingle, 1971), TBD 818, Alphard Formation, Agulhas Bank, Maastrichtian III. C. SAM-K5706, LV. D. SAM-K5707, internal LV. E. SAM-K5706, sieve plates over normal pore canal apertures LV. F. SAM-K5707, MS LV.

Scale bars: E-F = 10 μ , others = 100 μ .

are curious: there is an oval anterior scar and an irregular adductor formed by the fusion of a line of four oval scars.

Age, distribution, palaeoecology

Maastrichtian III (Alphard Formation, Agulhas Bank sample 818) (Fig. 22I). The ostracod assemblage of sample 818 is thought to represent an unusual setting: a quiet shallow-water environment at the outer edge of the continental shelf or on the uppermost continental slope.

Family **Cytherettidae?** Triebel, 1952

Genus ***Klingerella*** gen. nov.

Derivation of name

Named after Dr H. C. Klinger for his invaluable assistance during fieldwork in Zululand in 1977.

Type species

K. aranearius sp. nov.

Diagnosis

Elongate quadrate genus, ornamented with longitudinal ribs/reticulation, having a weakly developed amphidont hinge and very wide marginal areas.

Remarks

The style of the marginal areas of *Klingerella* suggests that it belongs within the family Cytherettidae, but its hinge, outline, MS and general ornamentation are reminiscent of many trachyleberids, and in this respect it has affinities with *Paracytheretta* Triebel, 1941, and *Neocytheretta* van Morkoven, 1963. It differs from these two genera in details of ornamentation and outline, particularly in lacking hinge ears and an obtuse posteroventral outline.

In general outline and ornamentation, *Klingerella* is closer to *Paracytheretta*, whereas its inner lamella and hinge are more like those of *Neocytheretta*. In addition, *Paracytheretta* appears to be blind, whereas *Klingerella* and *Neocytheretta* have eye spots. *Paracytheretta* has a range of Senonian to Palaeocene in Europe, and *Neocytheretta* has a range Miocene to Recent in the Indian Ocean and East Indies area.

Exclusively southern hemisphere genera with particularly wide marginal areas are *Paramunseyella* Bate (Santonian) and *Premunseyella* Bate (Santonian–Campanian) from Australia, but both differ from our new genus in possessing a typical pectocytherid outline, and in having pectodont hinges. *Klingerella* is so far known only from the Maastrichtian of south-east Africa.

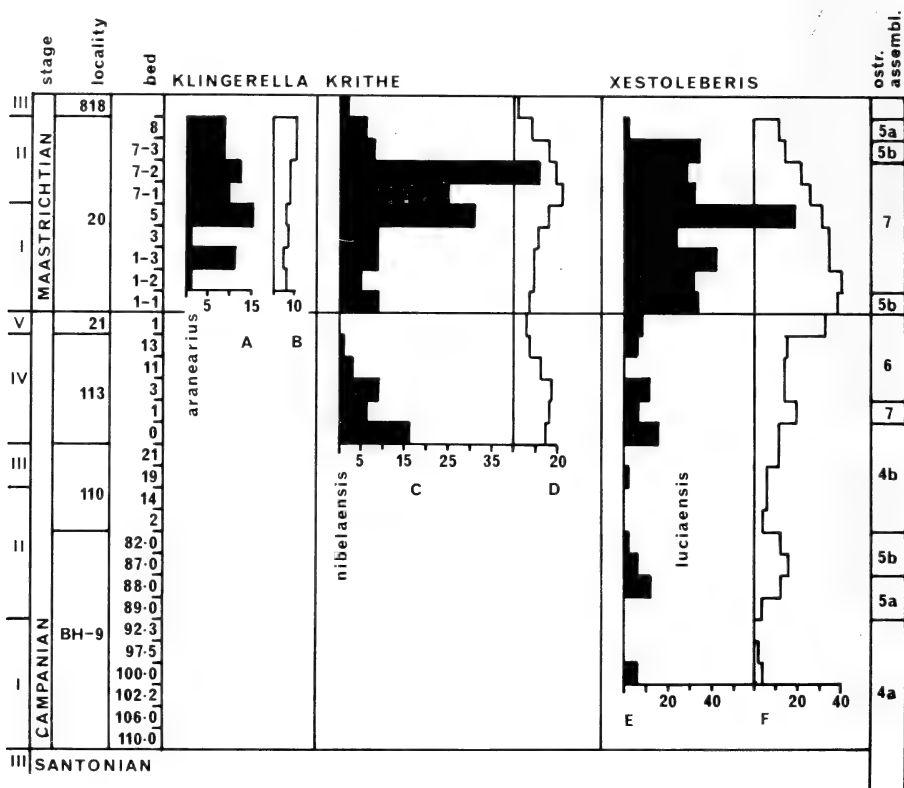


Fig. 27. Distribution of *Klingerella*, *Krithe*, and *Xestoleberis* in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Klingerella aranearius*. B. *Klingerella aranearius* as percentage of Cytheracea. C. Total number of valves of *Krithe nibelaensis*. D. *Krithe nibelaensis* as percentage of Cytheracea. E. Total number of valves of *Xestoleberis luciaensis*. F. *Xestoleberis luciaensis* as percentage of Cytheracea.

***Klingerella aranearius* sp. nov.**

Figs 28A–F, 29

Derivation of name

Latin *aranea* (spider's web): reference to spider's web-like reticulation pattern.

Holotype

SAM-K5708, LV, locality 20–5, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5709, RV, locality 20–5, Mfolozi River, Maastrichtian I

SAM-K5710, LV, locality 20–5, Mfolozi River, Maastrichtian I

SAM-K5711, RV, locality 20–5, Mfolozi River, Maastrichtian I

SAM-K5712, carapace, locality 20–5, Mfolozi River, Maastrichtian I

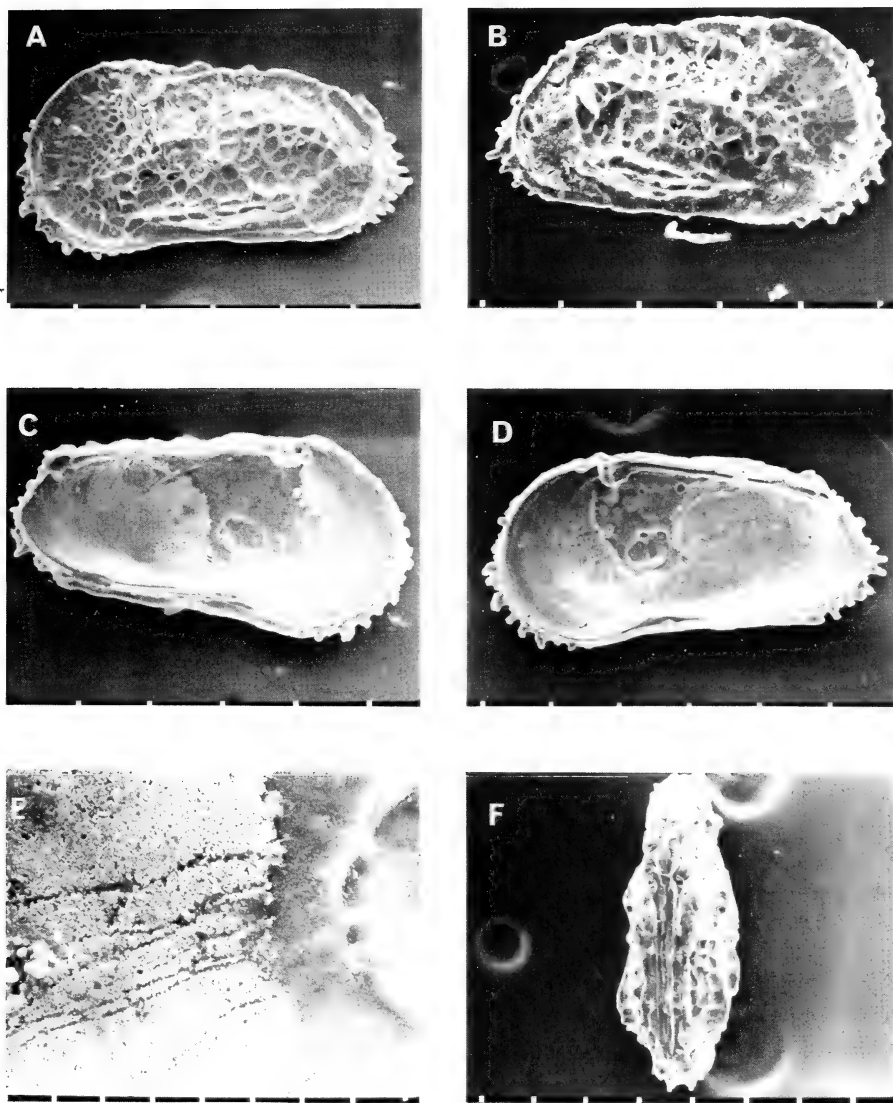


Fig. 28. *Klingerella aranearius* gen. et sp. nov. A. Holotype, SAM-K5708, LV. B. SAM-K5709, RV. C. SAM-K5710, internal LV. D. SAM-K5711, internal RV. E. SAM-K5710, detail inner edge of MA post-adjacent to MS pit LV. F. SAM-K5712, dorsal view carapace. All specimens from locality 20-5, Mfolozi River, Maastrichtian I.

Scale bars: E = 10µ, others = 100µ.

Diagnosis

Small species in which reticulation radiates from a subcentral site in a web-like mesh, and which possesses dorsal, ventral and incipient median ribs.

Description

External features. In lateral view outline quadrate, broadly rounded AM, obliquely rounded PM, and straight DM and VM. AM and PM are weakly spinose. Anterior area wide, compressed, with a prominent anterior marginal rim which continues dorsally over a small eye spot. Surface bears narrow but sharp dorsal and ventral ribs which are not joined to the AM. Ventral rib lies some way above VM, and is deflected upward posteriorly; dorsal rib commences at one-third length, is slightly convex upwards, and proceeds along the upper margin to join the PM just above mid height. There is an incipient median rib, best developed posteriorly, which in its more anterior part is merely a series of horizontal fossae muri. No SCT, but the surface reticulation forms a denser net over a low subcentral node (resembling the centre of a spider's web) away from which the reticulation muri radiate. One particularly prominent muri line runs a crooked course to the eye spot and another runs N-S, transverse to the median rib line. Reticulation is weakest in the anterior part of the valve. In dorsal view the carapace has a subtly waisted appearance about mid length. RV eye spot is more prominent than LV eye spot.

Internal features. Hinge weakly holamphidont with small peg-like ATE in RV and anterior part of LV ME. PTE more elongate. ME narrow and all elements are smooth. MS trachyleberid-like with a hooked, almost coiled, anterior scar and curved row of four oblong adductors, the top two of which are almost subdivided. There may be two further weak spots in the centre of the group. MA very wide, covering the entire inner surface except for the MS area and a short distance along the anterior dorsal margin. No vestibules. MPC hair-like and wavy, at least thirty in anterior area.

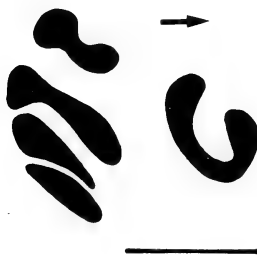


Fig. 29. Muscle scars, *Klingerella aranearius* gen. et sp. nov., SAM-K5710, locality 20-5, Mfolozi River, LV, Maastrichtian I.
Scale bar 30 μ .

Remarks

No other described species appears to be close to *K. aranearius*. *Paracytheretta reticosa* Triebel from the middle Palaeocene of Denmark has longitudinal ribs and reticulation, but has a different LV outline, and *Neocytheretta snellii* (Kingman) from the Recent of Indonesia has similar MA and hinge. Both of these species differ in important aspects of either internal features or external morphology.

In south-east Africa, *Klingerella aranearius* locally becomes an important and typical member of the cytheracean population (>10%) and for this reason has been selected as a subzonal marker in the upper part of the *Dutoitella dutoiti* Zone.

Dimensions (mm)

	length	height	width
K5708	0,52	0,28	
K5709	0,48	0,26	
K5710	0,52	0,27	
K5711	0,53	0,27	
K5712	0,58		0,21

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *K. aranearius* occurs in moderate numbers in ostracod assemblages 5a, 5b, and 7, indicating that it inhabited quiet environments ranging from ?200 to >500 m (mid shelf to upper slope) (Fig. 27A–B). It seems to have preferred the shallower water end of this range (?200–300 m).

Family **Progonocytheridae** Sylvester-Bradley, 1948

The poor representation of this family in the Upper Cretaceous rocks of south-east Africa is something of a puzzle in view of its strong presence in the Jurassic–Lower Cretaceous of the Western Indian Ocean area (east Africa, Madagascar, south-east Africa) with *Majungaella* and *Progonocythere*. The *Majungaella*/*Tickalaracythere* group is found in the Santonian–Campanian of Western Australia, but does not occur in south-east Africa (see Krömmelbein 1972).

Genus *Hutsonia* Swain, 1946*Hutsonia?* sp. A

Fig. 30A

Remarks

One poorly preserved carapace of this species was found in the Igoda section. It has the typical pyriform shape and reticulate ornamentation for the

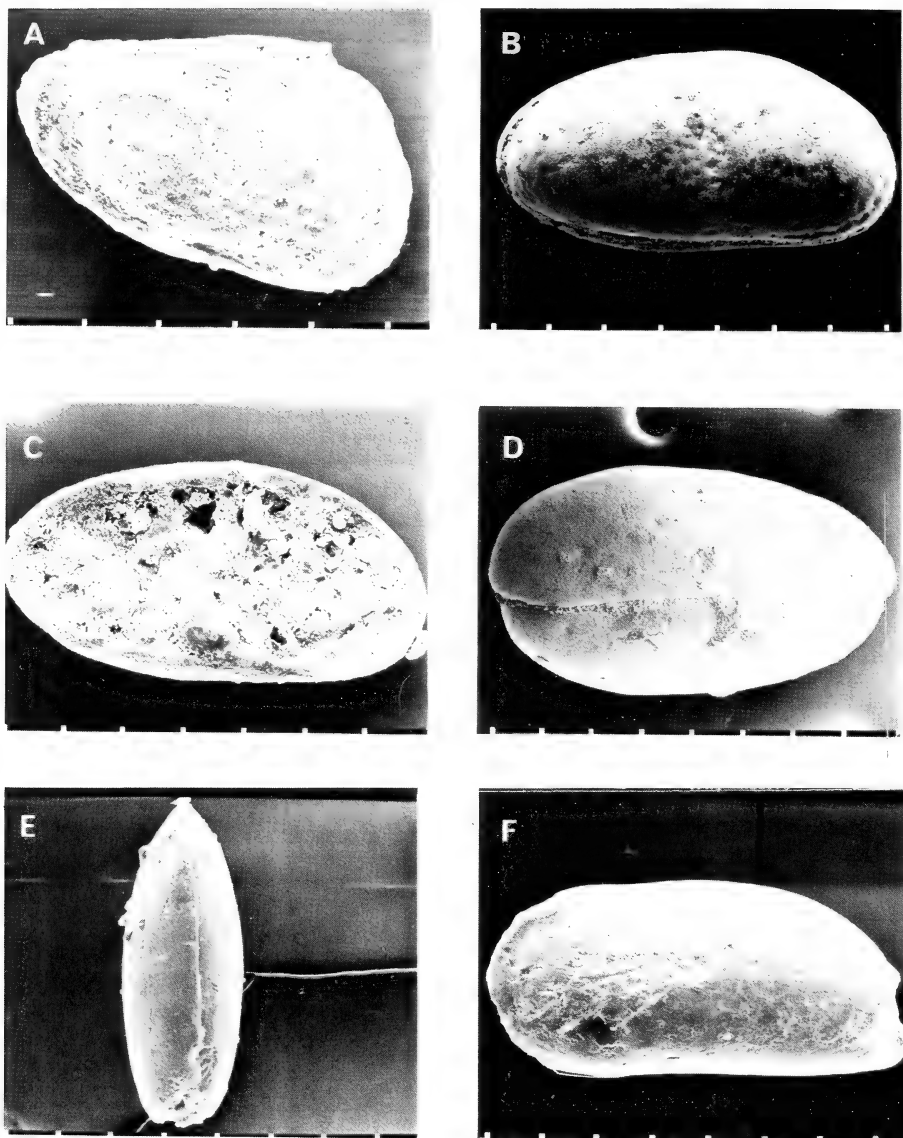


Fig. 30. A. *Hutsonia*? sp., SAM-K5713, Igoda Formation, Igoda estuary, RV, late Campanian/early Maastrichtian. B-D. *Pondoina igodaensis* sp. nov. Igoda Formation, Igoda estuary, late Campanian/early Maastrichtian. B. Holotype, SAM-K5714, RV. C. SAM-K5715, internal LV. D. SAM-K5716, dorsal view carapace, anterior is to the right. E-F. *Krithe* sp. E. SAM-K5717, JC-1 1625 m, dorsal view carapace, Maastrichtian. F. SAM-K5718, JC-1 1743 m, LV, Maastrichtian.

Scale bars all 100 μ .

genus, and possesses a median sulcus. Its hinge and MS could not be seen. *Hutsonia* is typical of very shallow marine conditions and has so far been positively recorded only from the upper Jurassic–Aptian of the east coast of the North American province. If substantiated, its presence in south-east Africa would greatly extend its known geographical and temporal range.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian (Igoda). The Igoda palaeosedimentary environment is considered to have been low-energy, normal marine, moderate water depth (~100 m inner shelf).

Family **Cytherideidae** Sars, 1925

Genus *Krithe* Brady, Crosskey & Robertson, 1874

Krithe is considered to be a marker for relatively deep-water sedimentary environments: e.g. ‘most common in infra-neritic and bathyal environments’ (Van Morkhoven 1963: 340) and its absence from the upper, deep-water faunas of the Richards Bay BH-9 borehole was considered by Dingle (1980) somewhat anomalous. The present work has located the genus in younger sequences than those available from BH-9, and extends the local range down into the upper Campanian. It had previously been recorded in moderate numbers in the Lower Palaeocene–Oligocene of the JC-1 borehole off-shore Natal (Dingle 1976) and has now been recorded sporadically in the Maastrichtian. No species of *Krithe* have been found at Igoda or Needs Camp. Significantly, Neale (1975) did not record the genus in the Santonian of Western Australia which he reckoned had been deposited in water depths of 80–100 m and Bate (1972) recorded only a few fragments from the Campanian of the Carnarvon Basin.

There are no records of it from the Upper Cretaceous of west Africa or Argentina, but Bate (*in* Bate & Bayliss 1969) notes its presence in small numbers in the Campanian and Maastrichtian of Tanzania.

***Krithe nibelaensis* sp. nov.**

Fig. 31A–F

Derivation of name

Locality of type.

Holotype

SAM-K5719, RV, locality 113–3, Nibela, Campanian IV

Paratypes

SAM-K5720, LV, locality 113–0, Nibela, Campanian IV

SAM-K5721, carapace, locality 113–0, Nibela, Campanian IV

SAM-K5722, LV, locality 113–3, Nibela, Campanian IV

SAM-K5723, carapace, locality 113–0, Nibela, Campanian IV

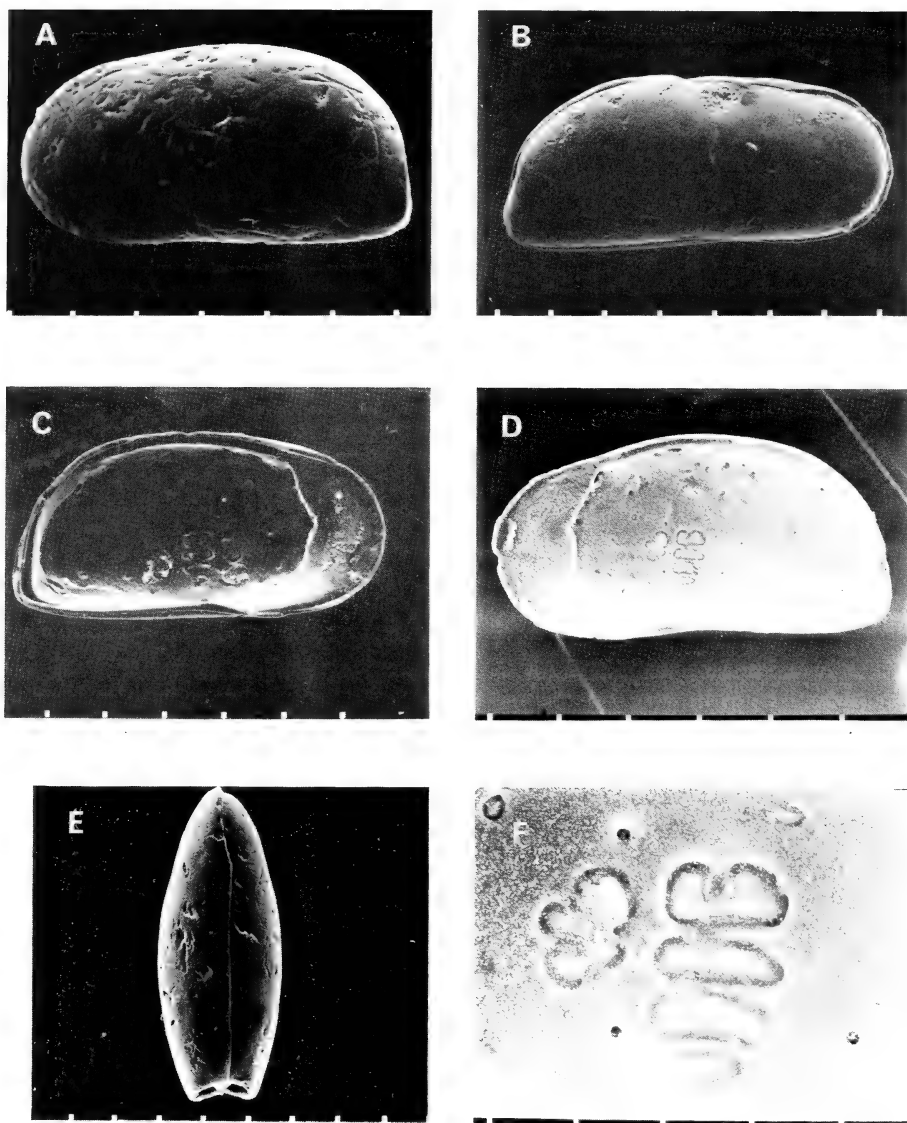


Fig. 31. *Krithe nibelaensis* sp. nov. A. SAM-K5720, locality 113-0, Nibela Peninsula, LV, Campanian IV. B. SAM-K5721, locality 113-0, Nibela Peninsula, RV, Campanian IV. C. SAM-K5722, locality 113-3, Nibela Peninsula, internal LV, Campanian IV. D. Holotype, SAM-K5719, locality 113-3, Nibela Peninsula, internal RV, Campanian IV. E. SAM-K5723, locality 113-0, Nibela Peninsula, dorsal view carapace, Campanian IV. F. Holotype, SAM-K5719, locality 113-3, Nibela Peninsula, MS RV, Campanian IV.

Scale bars: F = 30 μ , others = 100 μ .

Diagnosis

Slim species with star-shaped anterior MS.

Description

External features. In lateral view symmetrically rounded AM, acuminate PM. DM slightly convex, VM straight. Greatest height behind mid length. Outline in dorsal view slim, with posterior indentations clearly visible, and separated by a narrow bar.

Internal features. MA typical of the genus, wide anteriorly with a central, narrow vestibule that extends almost to AM. MPC not well developed, up to 4 anteriorly, 8 ventrally, and 3 posteriorly. MS consist of a stellate anterior scar and four oblong adductors. The lower adductor is small and oval, the central two oblong, and the upper more quadrate, with a dorsal incision which almost cuts it in half.

Remarks

K. nibelaensis has all the characters typical of the genus and as such is similar to many other species. Its distinctive features are its stellate anterior MS and its morphology in dorsal view. The genus has not been widely recorded from southern hemisphere Cretaceous strata: Bate (1972) mentions three specimens only (from the Lower Campanian of Western Australia, only one of which has the characteristic posterior indentation); and from various DSDP sites in the western South Atlantic (e.g. Benson 1977). Unfortunately, the latter have not yet been illustrated.

Our species is close to *K. rocana* Bertels (1973) from the early Danian of Argentina, but differs in being slimmer in dorsal view (length:width ratio of 2,59 compared to 2,34) and in having more prominent and deeply incised posterior indentations.

Although the species recorded from the Palaeocene–Oligocene of the JC–1 borehole by Dingle (1976) was not formally described, it is not conspecific with *K. nibelaensis* (see Dingle 1976, pl. 12(44)).

Dimensions (mm)

	length	height	width
K5719	0,55	0,27	
K5720	0,60	0,31	
K5721	0,70	0,30	
K5722	0,61	0,31	
K5723	0,70		0,27

Age, distribution, palaeoecology

Campanian IV to Maastrichtian III (Nibela and Mfolozi River, Zululand, and Agulhas Bank). *K. nibelaensis* has been found in all the deeper water assemblages in the Zululand outcrops, i.e. 5a, 5b, 6–7, and in one sample in

assemblage 4b (Fig. 27C–D). This distribution suggests that it inhabited water depths of ?200 to >500 m (mid shelf to upper slope) but with a preference for the deep stable (>500 m), outer shelf/upper continental slope environments where it locally reaches >20 per cent of the Cytheracea population. In the somewhat more unstable upper slope environment represented by ostracod assemblage 6, it is consistently present at >15 per cent. The non-appearance of species of *Krithe* in the Campanian II (ostracod assemblage 5a, 5b)) still cannot be satisfactorily explained.

Krithe sp. A

Fig. 30E–F

Remarks

Four specimens of *Krithe* have been recovered from borehole JC–1 which are probably not conspecific with either *Krithe nibelaensis* (Campanian–Maastrichtian of Zululand and Agulhas Bank) or *Krithe* sp. 1 and *K.* sp. 2 (Palaeocene–lower Oligocene of higher sections of JC–1 borehole (Dingle, 1976)). However, because no satisfactory internal views were available, the absence of the stellate anterior scar in *K. nibelaensis* could not be confirmed. *K.* sp. A and *K. nibelaensis* differ most notably in the shape of the posterior indentation in dorsal view—in the former it is larger and more acute. *K.* sp. 1 and *K.* sp. 2 have different AM outlines to *K.* sp. A. The status of the species is uncertain until more material becomes available.

Age, distribution, palaeoecology

Occurs in four samples in the Maastrichtian of JC–1 borehole, between levels 1 625 m and 1 743 m. Only one of these levels coincides with horizons in which charophytes is found and the species always occurs in association with one or two of the following genera: *Bairdoppilata*, *Cytherella* or *Bythocypris*?. Such a distribution is consistent with the known preference of *Krithe* for deeper water environments and its presence may be helpful in identifying periods of deepening and/or shallowing on the Tugela Delta top (see Table 10 and discussion section).

Genus *Pondoina* Dingle, 1969

This genus is represented in the Santonian strata of south-east Africa by *P. sulcata* which reaches 10 per cent of the total ostracod population at Umzamba. The same species is present in small numbers in the Santonian III of the Richards Bay BH–9 borehole, but does not range into the Campanian. The only record of *Pondoina* in the Campanian–Maastrichtian rocks of south-east Africa is at Igoda. Krömmelbein (1972) records species tentatively assigned to *Pondoina* from the Turonian Sibang Formation of Gabon and the ?Coniacian Macaú Formation of north-east Brazil.

Pondoina igodaensis sp. nov.

Fig. 30B–D

Derivation of name

Locality of type.

Holotype

SAM–K5714, carapace, Igoda Formation, Igoda Estuary, late Campanian/early Maastrichtian

Paratypes

SAM–K5715, LV, Igoda Formation, Igoda Estuary, late Campanian/early Maastrichtian

SAM–K5716, carapace, Igoda Formation, Igoda Estuary, late Campanian/early Maastrichtian

Diagnosis

Plump species with strongly asymmetric AM outline in LV.

Description

External features. In lateral view, AM asymmetrically rounded. PM narrower, symmetrically rounded. DM gently arched. VM in RV nearly straight or slightly concave in anterior third in LV convex. Highest point of valve at about one-third length. In dorsal view LV distinctly larger than RV, plump appearance with maximum width at about two-thirds length. There is a weak, vertical median sulcus which gives a subtly waisted outline in dorsal view. Surface smooth with shallow rounded pits concentrated in the vicinity of the median sulcus and the anterior border.

Internal features. Hinge antimerodont. MS and MA not seen.

Remarks

P. igodaensis differs from *P. sulcata* by its plumper shape and asymmetrical LV AM outline.

Dimensions (mm)

	length	height	width
K5714	0,69	0,36	
K5715	0,70	0,38	
K5716	0,80		0,45
Other material	0,81	0,48	

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian (Igoda Formation). The Igoda palaeosedimentary environment is considered to have been low-energy, normal-marine, moderate-water depth (~100 m, inner shelf).

Family **Xestoleberididae** Sars, 1928Genus *Xestoleberis* Sars, 1866***Xestoleberis luciaensis*** sp. nov.

Fig. 32A–G

Xestoleberis sp. A Dingle, 1980: 19–20, fig. 8A–B.*Derivation of name*

Locality of type—Nibela Peninsula, Lake St Lucia.

Holotype

SAM-K5724, RV, locality 20–5, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5725, RV, locality 20–1/3, Mfolozi River, Maastrichtian I

SAM-K5726, LV, locality 20–1/3, Mfolozi River, Maastrichtian I

SAM-K5727, RV, locality 20–1/3, Mfolozi River, Maastrichtian I

Diagnosis

Plump species, with all hinge elements crenulate and MS that consist of two antennal scars and four adductors, the top one being almost subdivided.

Description

External features. In lateral view, asymmetrically rounded AM with an angular, 'beaked' overhang in the anteroventral area of the RV. VM convex, DM strongly arched. Greatest height behind mid length. PM broadly rounded. In some specimens there is a very weakly developed AM rim in the LV. Valve surface smooth except for occasional NPC openings and faint ridges in the anteroventral extremity.

Internal features. Hinge strongly antimerodont with a small DM projection above ME in RV and ATE in LV. MS consist of four elongate adductors, the top one being almost bisected, and two antennal scars: a small rounded scar within a large sickle-shaped scar. The 'xestoleberis spot' is well developed. MA moderately wide anteriorly, narrow posteriorly. Wide anterior vestibules with apparently few (?up to six) anterior MPC. Posterior MPC could not be counted, and despite the large numbers of specimens available the number quoted for anterior MPC is not definite. There are numerous NPC on the interior surface but few appear to open to the exterior.

Remarks

Because *X. luciaensis* has all the characters of the genus, it is close to many other species, but can be distinguished in well-preserved specimens on details of hingement and MS. *X. luciaensis* appears to be the first Mesozoic species recorded from the southern hemisphere, but Neufville (1979) has described 'Danian' species from the Sergipe Basin of eastern Brazil. His closest form is *X.*

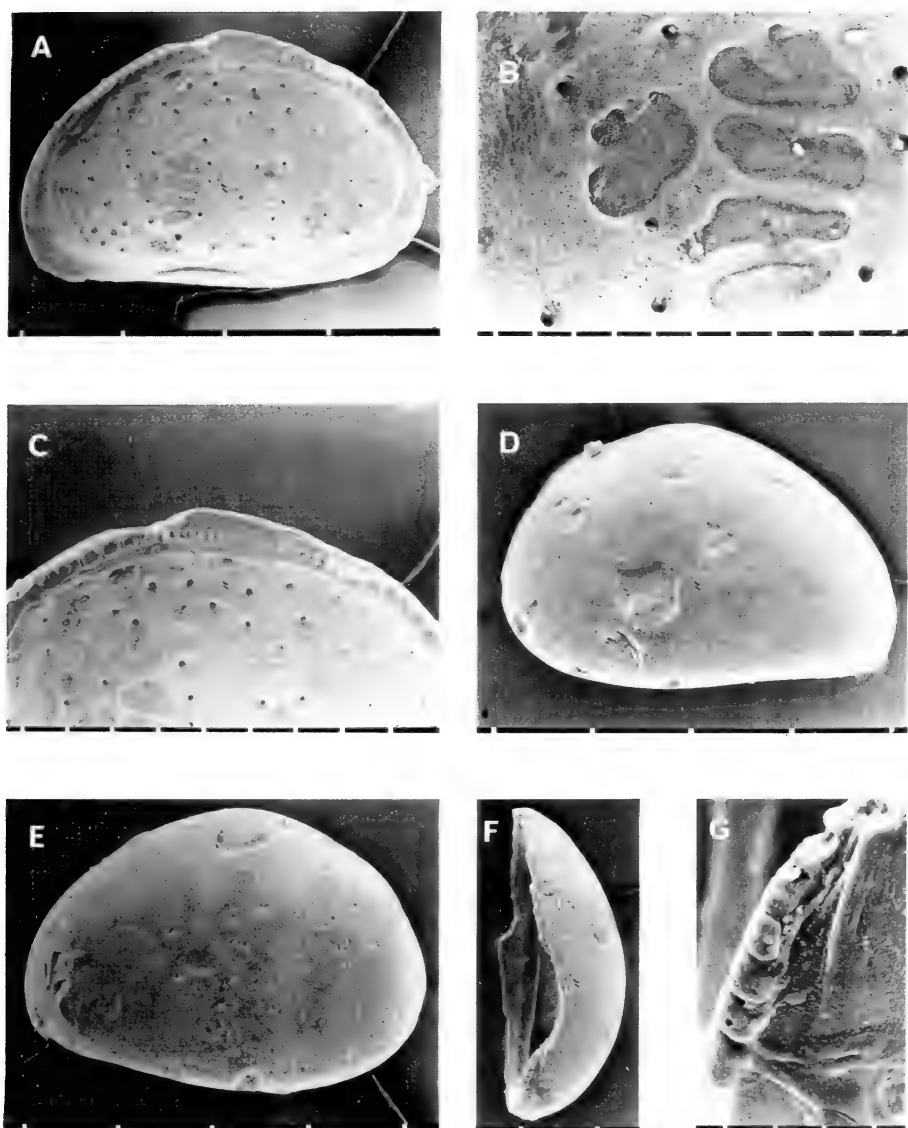


Fig. 32. *Xestoleberis luciaensis* sp. nov. A-C. Holotype, SAM-K5724, locality 20-5, Mfolozi River, internal RV(A) MS(B) hinge (C), Maastrichtian I. D. SAM-K5725, locality 20-1/3, Mfolozi River, RV, Maastrichtian I. E. SAM-K5726, locality 20-1/3, Mfolozi River, LV, Maastrichtian I. F-G. SAM-K5727, locality 20-1/3, Mfolozi River, dorsal view RV(F) detail PTE(G), Maastrichtian I.

Scale bars: B; G = 10μ , C = 30μ , others = 100μ .

chamela van den Bold, which is less plump in dorsal view and somewhat less angular in its anteroventral outline than *X. luciaensis*.

Dimensions (mm)

	length	height	width
K5724	0,40	0,25	
K5725	0,40	0,27	
K5726	0,42	0,30	
K5727	0,40		0,13

Age, distribution, palaeoecology

Companian I to Maastrichtian II (Zululand: Richards Bay BH-9 borehole and Monzi, Mfolozi, and Nibela outcrops). *X. luciaensis* is an environmentally tolerant species that has been found in ostracod assemblages 4a, 4b, 5a, 5b, 6-7 (Fig. 27E-F, Table 4). Its preference, in increasing compatibility within these, would seem to be (values are mean % cytheracean population): 4a (~2%), 4b and 5a (4-7%), 6 (~20%), 5b (~25%), and 7 (~30%). The significant values here are: (i) a sharp increase in populations that are thought to represent deep-water environments (ie >300 m), (ii) main preference for assemblage 7 which represents stable environments >500 m (outer shelf/upper continental slope).

Family **Buntoniidae** Apostolescu, 1961

Genus *Buntonia* Howe, 1935 (in Howe & Chambers 1935)

Buntonia? sp. A

Fig. 34A

Remarks

A carapace referred to *Buntonia* on the grounds of its shape, particularly its upturned posterior outline. Features not conforming to typical species of this genus are: lack of eye spot, and smooth posterior area (which typically bears small longitudinal ribs). *Buntonia* is common in the uppermost Cretaceous of west Africa, and has been recorded from the upper Eocene of the JC-1 borehole (Dingle 1976), but no positive identifications have yet been made in the Cretaceous of south-east Africa.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian (Igoda Formation, Igoda). The Igoda palaeosedimentary environment is considered to have been low-energy, normal-marine, moderate-water depth (~100 m, inner shelf).

Family **Brachycytheridae** Puri, 1954

In diversity and consistency of distribution, the Brachycytheridae (jointly with the Schizocytheridae) rank second in importance within the families of the Cytheracea (Table 17b). Numerically, however, the Brachycytheridae are far more important than the Schizocytheridae: in Campanian I the former consti-

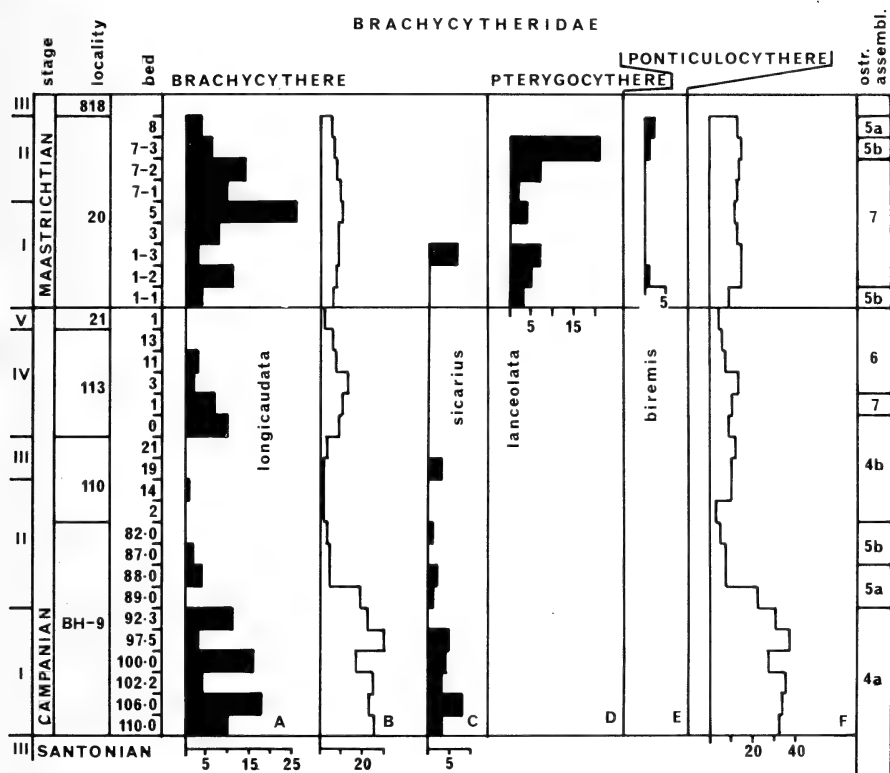


Fig. 33. Distribution of Brachycytheridae in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Brachycythere longicaudata*. B. *Brachycythere longicaudata* as percentage of Cytheracea. C. Total number of valves of *Brachycythere sicarius*. D. Total number of valves of *Pterygocythere lanceolata*. E. Total number of valves of *Ponticulocythere biremis*. F. Total Brachycytheridae as percentage of Cytheracea.

tutes ~30 per cent of the Cytheracea, and in Campanian II to Maastrichtian II 10–20 per cent (compare Figs 22K and 33F).

The family is represented by three genera and four species: *Brachycythere longicaudata*, *B. sicarius*, *Pterygocythere lanceolata*, and *Ponticulocythere biremis*. Only *Brachycythere* occurs in the Campanian and Maastrichtian (both species are inherited from the Santonian), whilst *Pterygocythere* and *Ponticulocythere* are restricted to the Maastrichtian.

Genus *Brachycythere* Alexander, 1933
Brachycythere longicaudata (Chapman, 1904)

Fig. 34B–C

Cytheridea longicaudata Chapman, 1904: 234–235, pl. 29 (fig. 21). Howe & Laurencich, 1958: 279.

Cythere ?drupracea Jones, 1884, Chapman, 1904: 234.

Brachycythere longicaudata (Chapman), Dingle, 1969: 358–361, fig. 7. Dingle, 1980: 25–26, figs 12A–C, 13A–D.

Remarks

B. longicaudata exhibits a good deal of intraspecific morphological variation, and the specimens from Igoda are closest to the more elongate forms at Umzamba (type horizon), though they are slightly smaller. Bate (*in* Bate & Bayliss 1969) illustrates a form which he assigns to *B. aff. B. sapucariensis* Krömmelbein, 1964, from the Turonian of Tanzania. Within the limits of his sketch, this specimen could easily be accommodated within *B. longicaudata* (compare Bate 1969, pl. 7 (fig. 1) with Dingle 1980, fig. 12B).

Age, distribution, palaeoecology

Santonian II to Maastrichtian II (Umzamba, and Richards Bay BH-9 borehole, and Mfolozi and Nibela outcrops in Zululand), late Campanian/early Maastrichtian (Igoda).

Dingle (1980) found this to be the most common species of ostracod in the Richards Bay BH-9 borehole, particularly in the lower, Santonian part, where it locally constituted 88 per cent of the cytheracean population (~50% total population). Although its importance declines up the borehole into the lower Campanian, it occurs sporadically throughout the whole of the Campanian-Maastrichtian in Zululand. It is one of the most environmentally-tolerant ostracod species in the south-east African upper Cretaceous and has been found in ostracod assemblages 1-3, 4a, 4b, 5a, 5b, 6-7 (Fig. 33A-B, Table 4). As shown in Figure 33B, its importance (expressed as a percentage of the cytheracean population) varies between 16 and 62 per cent in water reckoned to be shallower than about 200 m, but drops sharply to between 3 and 10 per cent in deeper water environments. It preferred the high-energy, restricted circulation, shallow water of assemblage 1 (Santonian II, Richards Bay BH-9 borehole), but curiously stages an 'ecological recovery' in the deep water (>500 m) of assemblages 6 and 7, compared with the low values and sporadic distribution in the moderate depth (200-400 m) mid-shelf environments. A somewhat similar phenomenon was noted in the case of *Cythereis klingerii*. A possible explanation is of posthumous transportation into deep water by currents.

At Igoda, *B. longicaudata* constitutes 26 per cent of the cytheracean population.

Brachycythere sicarius Dingle, 1980

Fig. 35A

Brachycythere sicarius Dingle, 1980: 27-29, figs 13E, 14A-F.

Remarks

This species has been located at only two horizons above the stratigraphic level of the Richards Bay BH-9 borehole (Fig. 33C).

Age, distribution, palaeoecology

Santonian II to Maastrichtian I (Richards Bay BH-9 borehole and, Mfolozi and Nibela outcrops). *B. sicarius* occurs only sporadically in the Upper Cre-

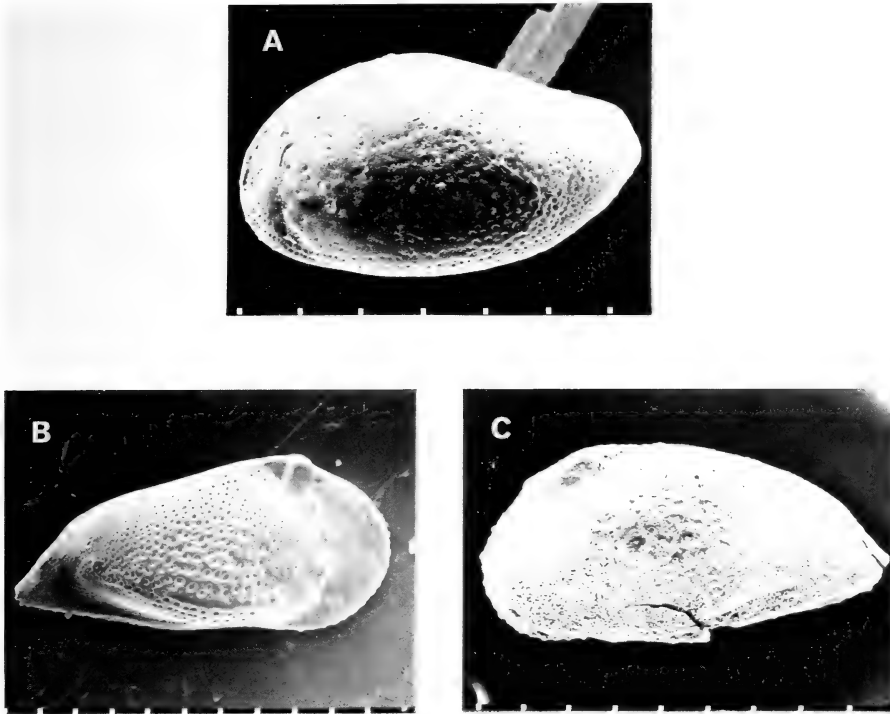


Fig. 34. A. *Buntonia?* sp., SAM-K5728, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian. B–C. *Brachycythere longicaudata* (Chapman, 1904). B. SAM-K5603, BH9 106,2 m, RV, Campanian I. C. SAM-K5729, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian.
Scale bars 100 μ .

taceous of south-east Africa, but has been found in the following assemblages: 1–3, 4a, 4b, 5a, 5b, and 7. Appearances in the deep-water assemblages 5b and 7 are confined to single samples and the species clearly preferred the moderate depth (?100–200 m inner-mid shelf) environments represented by assemblage 4a, although even here it is generally insubordinate in numbers to its close relative *B. longicaudata*.

Genus *Pterygocythere* Hill, 1954
Pterygocythere lanceolata sp. nov.
 Fig. 35B–F

Derivation of name

Reference to lance-like spine on ventrolateral alae.

Holotype

SAM-K5730, LV, locality 20–1/3, Mfolozi River, Maastrichtian I

Paratypes

- SAM-K5731, carapace, locality 20-1/2, Mfolozi River, Maastrichtian I
 SAM-K5732, carapace, locality 20-1/3, Mfolozi River, Maastrichtian I
 SAM-K5733, LV, locality 20-1/2, Mfolozi River, Maastrichtian I
 SAM-K5734, RV, locality 20-1/1, Mfolozi River, Maastrichtian I

Diagnosis

Smooth-surfaced species with a posteriorly directed spine on alae terminations.

Description

External features. Triangular in lateral view, with marginal spines in posteroventral and anteroventral positions. AM broadly rounded, PM acuminate. DM and VM straight, converging strongly posteriorly. The surface is smooth, except for small punctae in the posterior part. Its most prominent feature is a large wing-like ala on each valve which has a sharp posteriorly directed terminal spine. There is a prominent eye spot and a small post-ocular sinus.

Internal features. Hinge amphidont. PTE and ME crenulate, ATE weakly subdivided with, in RV, a frilled spur on its anterior end. There is a deep ventrolateral sinus leading into the ala. MS consist of a hooked anterior scar and four adductor scars. MA moderately wide. MPC numerous, fine and straight: up to 20 anteriorly, about 9 posteriorly.

Remarks

Placed in *Pterygocythere* because of its strongly alate shape. However, in all other respects the species possesses the characters of local representatives of the genus *Brachycythere*: the hinge is identical to *B. longicaudata* and *B. sicarius* (the latter even has the frilled anterior rim in RV ATE) and the MS are identical to *B. longicaudata*. It differs from these two species in shape and ornamentation, but quite clearly is very closely related. From stratigraphic and morphological considerations it is probable that *P. lanceolata* developed from *B. sicarius*, which itself is an alate development of *B. longicaudata*. The new species has been placed in *Pterygocythere* rather than *Alatacythere* because of its prominent accommodation groove in the LV, a feature also common to the local *Brachycythere* species.

Dimensions (mm)

	length	height	width
K5730	0,75	0,45	
K5731	0,78		0,55
K5732	0,75	0,45	
K5733	0,70	0,40	
K5734	0,68	0,38	

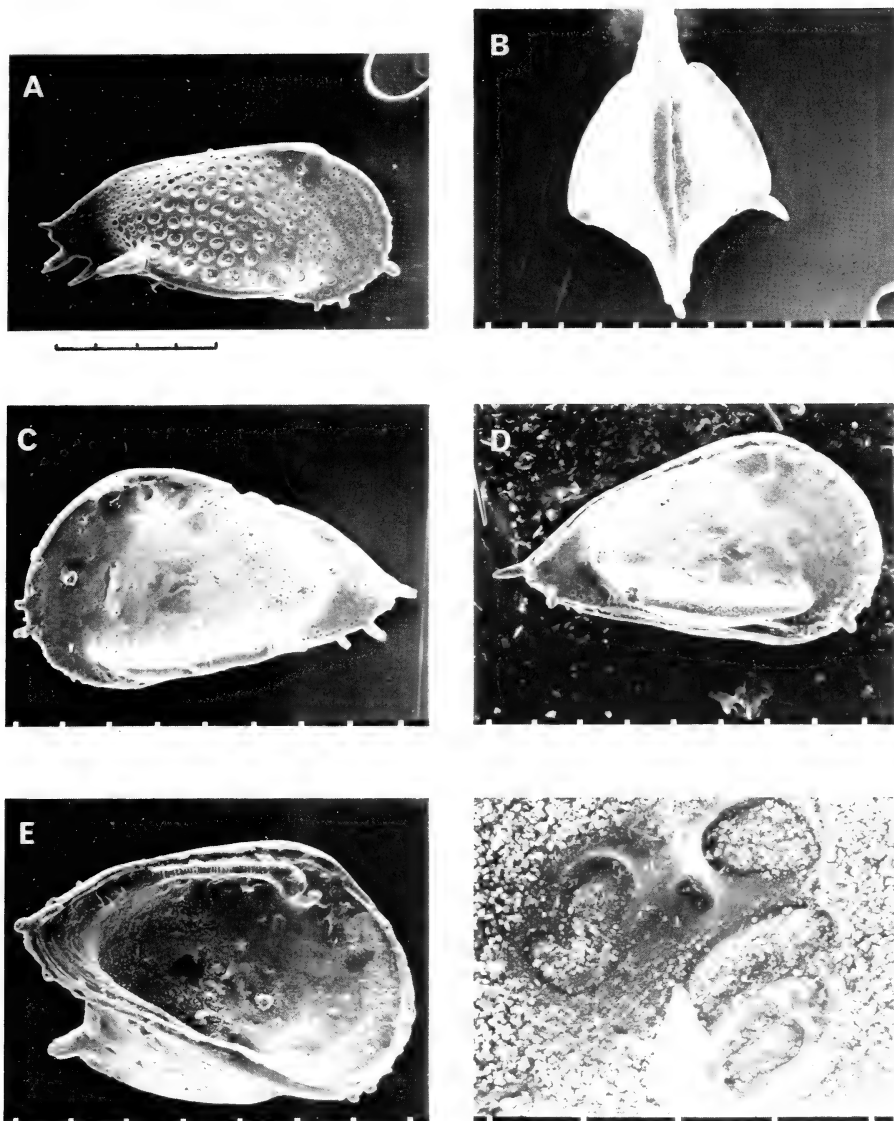


Fig. 35. A. *Brachycythere sicarius* Dingle, 1980, SAM-K5606, BH9 89,0 m, RV, Campanian II. B-F. *Pterygocythere lanceolata* sp. nov. B. SAM-K5731, locality 20-1/2, Mfolozi River, dorsal view carapace, Maastrichtian I. C. Holotype, SAM-K5730, locality 20-1/3, Mfolozi River, LV, Maastrichtian I. D. SAM-K5732, locality 20-1/3, Mfolozi River, RV, Maastrichtian I. E. SAM-K5733, locality 20-1/2, Mfolozi River, internal LV, Maastrichtian I. F. SAM-K5734, locality 20-1/1, Mfolozi River, MS RV, Maastrichtian I.

Scale bars: F = 30 μ , others = 100 μ .

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River Zululand) (Fig. 33D). *P. lanceolata* occurs in ostracod assemblages 5a, 5b, and 7, but preferred the quiet, deeper-water conditions of 5b and 7: ?300 m – >500 m (outer shelf to upper continental slope).

Genus *Ponticulocythere* gen. nov.*Derivation of name*

Latin *ponticulus* (a small bridge) + generic name *cythere*: reference to ponticulate lateral ribs.

Type species

Ponticulocythere biremis sp. nov.

Diagnosis

Subquadrate in lateral view with: ponticulate dorsal and ventral ribs; no median rib; eye spot; smooth or postulate intercostal areas; strong AM rim. Alate in dorsal view. Hinge entomodont or modified entomodont.

Remarks

The family placement of this genus is not certain. Externally it has features in common with *Ponticocythereis* McKenzie, 1967, which has a reported range Tertiary to Recent, with the genotype Recent from south-east Australia. McKenzie's species differs from *Ponticulocythere* in possessing a longitudinal lateral median ridge and in having a holamphidont hinge. Because *Ponticulocythere* has no median lateral rib, and does not have an amphidont hinge, it is not placed in the Trachyleberididae. Its alate appearance and hinge which, although entomodont, could be considered a modification of a weak amphidont structure, suggest that it has affinities with genera such as *Bosquetina* and *Pterygocythereis*. In the latter respect, *Ponticulocythere* is closer to *Bosquetina*, with the genotype and typical species of *Pterygocythereis* having holamphidont hinges. However, *Ponticulocythere* differs strongly from *Bosquetina* in their respective lateral architecture, in which it has affinities with *Pterygocythereis*. The main difference here is the spinose nature of the ribs in *Pterygocythereis* and their ponticulate aspect in *Ponticulocythere*. In the light of these similarities, the new genus is placed in the Brachycytheridae.

Age

It is known so far only from the Maastrichtian of south-east Africa.

Ponticulocythere biremis sp. nov.

Fig. 36A–E

Derivation of name

Latin *biremis* (galley with two banks of oars): fanciful reference to its appearance in lateral view.

Holotype

SAM-K5735, RV; locality 20-1/2, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5736, LV, locality 20-8, Mfolozi River, Maastrichtian II

SAM-K5737, RV, locality 20-7/3, Mfolozi River, Maastrichtian II

Diagnosis

Species with small post-ocular sail-like projection on DM, and coarse spines on posteroventral margin.

Description

External features. In lateral view subquadrate, broadly rounded AM, slightly acuminate PM with coarse posteroventral spines. DM and VM straight, converging only slightly posteriorly. DM hidden by curved ponticulate rib that commences post-adjacent to the large rounded eye spot and ends at the posterodorsal angle where it bears a small spine. There is a small pointed sail-like projection on the DM immediately behind the eye spot. Ventrolateral ponticulate rib abruptly joins the AM rim and posteriorly rises, ending at about three-quarters length. Central area smooth with occasional small perforate pustules and an indistinct swelling representing the SCT. Anterior area of the valve is somewhat compressed with large, ill-formed fossae in the AM rim. In dorsal view, arrow-shaped with ventrolateral ponticulate rib prominent along an alate projection. Widest part of valve in posterior third.

Internal features. MS not seen. MA apparently narrow, but this may be due to damage to valves. Hinge entomodont: RV has elongate dentate terminal elements, the PTE being more prominent than ATE in dorsal view. LV has a narrow, weakly dentate ME with a small, elongate anterior swelling, ATE consists of a shallow, anteriorly widening depression. LV PTE not seen.

Remarks

P. biremis is not closely related to any described species. Superficially it has features in common with several taxa with ponticulate, carinate or undercut clavae, for example: *Carinocythereis antiquata* (Baird), Recent; and *Ponticocythereis militaris* (Brady), Recent, but differs on essential points of generic morphology.

Dimensions (mm)

	length	height	width
K5735	0,82	0,40	
K5736	0,60	0,32	
K5737	0,58		0,18

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand) (Fig. 33E). *P. biremis* occurs in very small numbers in ostracod assemblages 5a, 5b, and 7. The

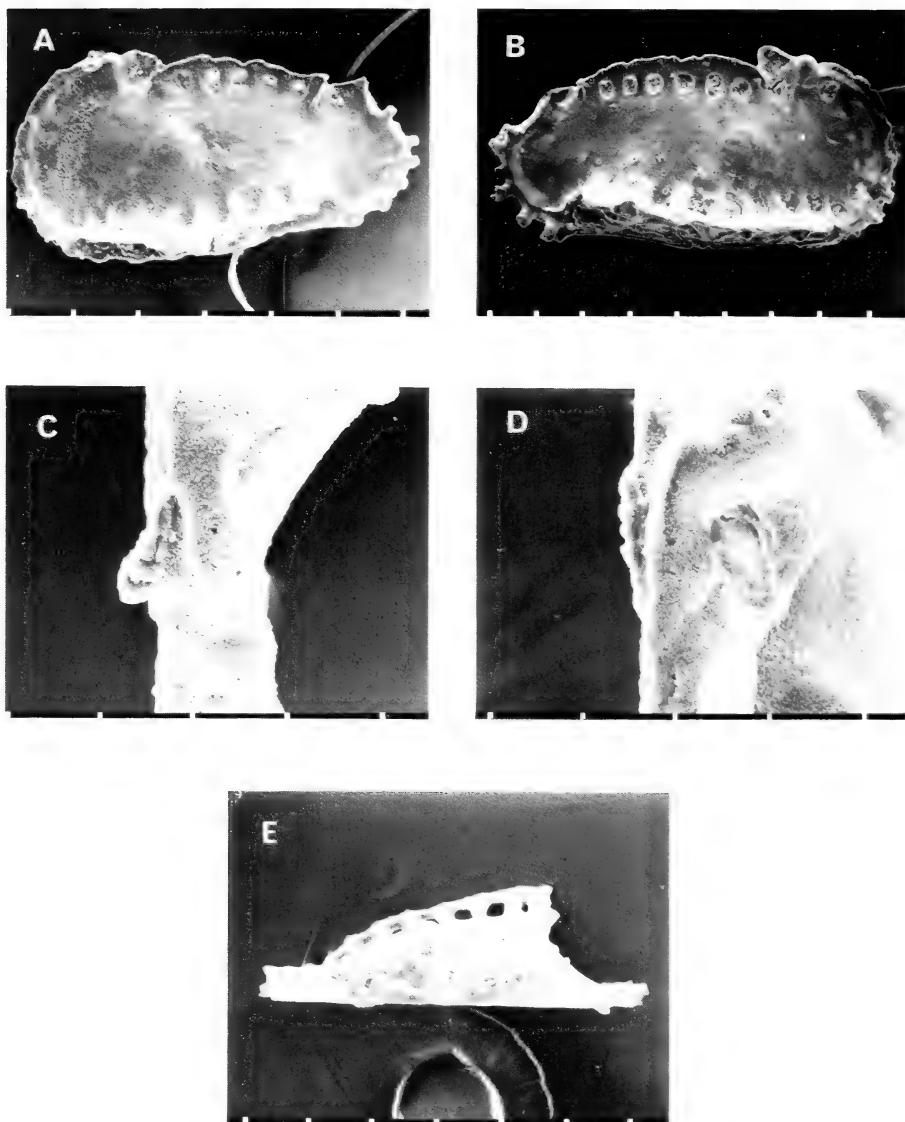


Fig. 36. *Ponticulocythere biremis* gen. et sp. nov. A. SAM-K5736, locality 20-8, Mfolozi River, LV, Maastrichtian II. B. Holotype, SAM-K5735, locality 20-1/2, Mfolozi River, RV, Maastrichtian I. C-E. SAM-K5737, locality 20-7/3, Mfolozi River, ATE dorsal view (D) PTE dorsal view (C) dorsal view RV(E), Maastrichtian II.
Scale bars: C-D = 30 μ , others = 100 μ .

sparse data available suggest that the species preferred the quiet-water moderate depths (?200–500 m mid-outer shelf) represented by assemblage 5.

Family **Trachyleberididae** Sylvester-Bradley, 1948

In terms of numbers of species, the Trachyleberididae is the most important cytheracean family in the Campanian–Maastrichtian rocks of south-east Africa. Only in the deep-water environments, represented by assemblages 5b, 6 and 7, does it numerically fall below 40 per cent, and have a diversity (number of species) below 50 per cent of the total cytheracean populations (see Table 17).

Subfamily **Pennyellinae** Neale, 1975

Neale (1975) separated a group of strongly reticulate, blind genera of trachyleberid-type in which he placed the following taxa: *Pennyella* (Santonian–Maastrichtian), *Agulhasina* (Maastrichtian) and *Agrenocythere* (Eocene–Recent). In the Upper Cretaceous, these genera are confined to the South Africa–Australia–West Pacific area, but from the Oligocene onwards, *Agrenocythere* develops into a deep-water cosmopolitan genus. Genus B. described by Bate (*in* Bate & Bayliss 1969) from the Campanian of Tanzania may also belong here.

Genus *Agulhasina* Dingle, 1971

Despite the availability of more material from the Upper Cretaceous of south-east Africa, the genus remains monospecific and confined to the Maastrichtian III of the Agulhas Bank, suggesting that it developed late in the Maastrichtian. However, Genus B of Bate (*in* Bate & Bayliss 1969) is superficially similar to the genotype, raising the possibility that *Agulhasina* in fact originated during the Campanian in the east Africa area. The phylogeny of the genus is at present, therefore, unknown.

Agulhasina quadrata Dingle, 1971 Figs 37A–B, 44A

Agulhasina quadrata Dingle, 1971: 414–416, fig. 15, Pl. VII(b).

Remarks

Additional work on specimens from sample 818 on the Agulhas Bank allows a more detailed presentation of valve morphology and MS patterns than was possible in the original description. The MS pattern of *Agulhasina quadrata* (Fig. 44A) differs from that of *Pennyella pennyi* in having a kidney-shaped anterior scar (the latter has a V-shaped scar), and in having two small rounded scars in the lower positions of the posterior row, rather than elongate scars as in *Pennyella*. Also, under high magnification, the indistinct SCT of *Agulhasina quadrata* is seen to have two short median ribs (about 50 μ long) on its posterior end.

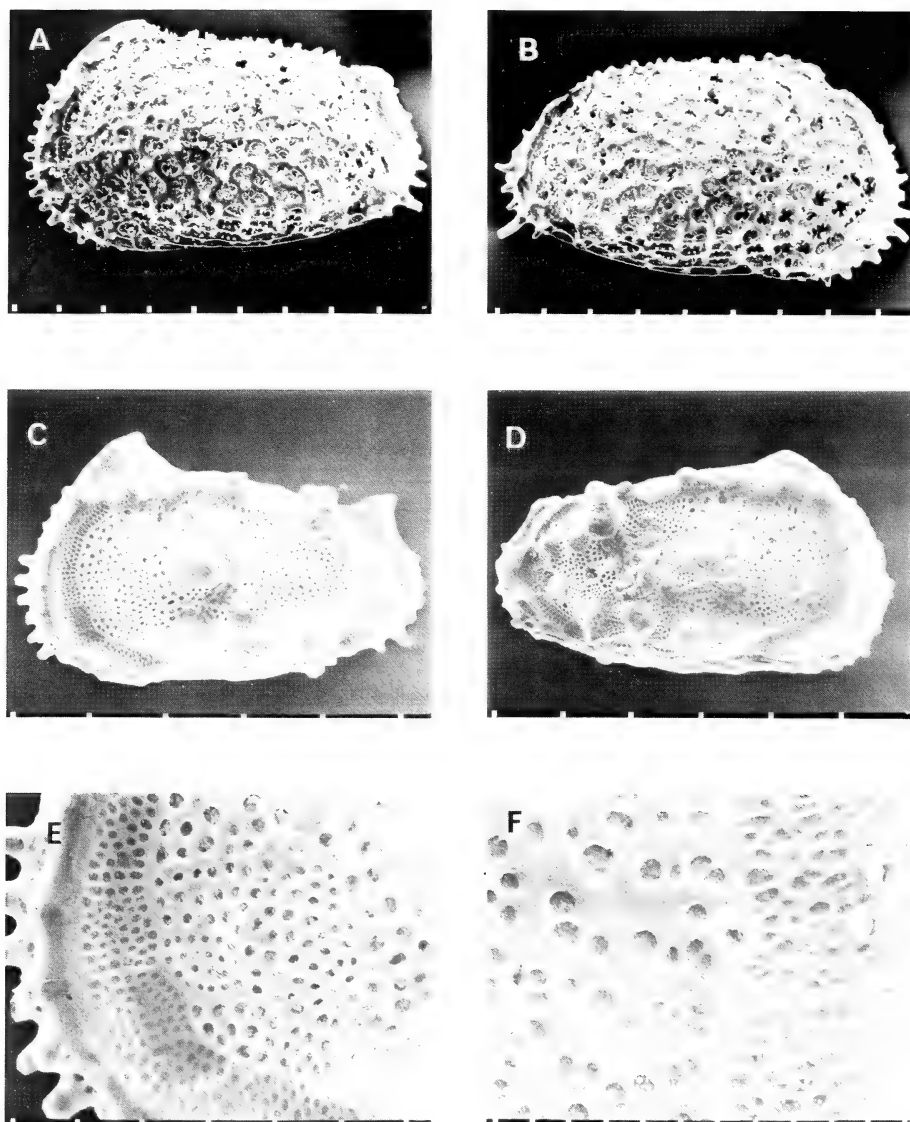


Fig. 37. A-B. *Agulhasina quadrata* Dingle, 1971, TBD, 818 Alphard Formation, Agulhas Bank, Maastrichtian III. A. SAM-K5738, LV. B. SAM-K5739, RV. C-E. *Unicapella sacsi* Dingle, 1980. C. SAM-K5740, locality 20-7/1, Mfolozi River, LV, Maastrichtian II. D. SAM-K5741, locality 21-1, Monzi, RV, Campanian V. E. SAM-K5740, locality 20-7/1, Mfolozi River, detail anterior area LV, Maastrichtian II. F. *Dutoitella mimica* gen. et sp. nov., SAM-K5748, TBD 818 Alphard Formation Agulhas Bank, detail anterior area RV, Maastrichtian III.

Scale bars: E = 30 μ , F = 10 μ , others = 100 μ .

Age, distribution, palaeoecology

A. quadrata is known only from the Maastrichtian III (sample 818) on the Agulhas Bank, and because of its distinctiveness it has been selected as the zonal ostracod for the *A. quadrata* Zone. The assemblage of sample 818 is thought to represent an unusual setting: quiet, shallow-water environment on the outer edge of the continental shelf or on the uppermost continental slope.

Subfamily **Unicapellinae** subfam. nov.*Type genus*

Unicapella Dingle, 1980 (Santonian–Maastrichtian).

Other genera

Dutoitella gen. nov. (Campanian–Maastrichtian), *Paleoabyssocythere* Benson, 1977 (Campanian–Palaeocene), *Atlanticythere* Benson, 1977 (Campanian–Miocene), *Herrigocythere* Gründel, 1973 (Campanian–?Maastrichtian).

Diagnosis

Blind, weakly reticulate to foveolate genera of general trachyleberid aspect with prominent domed or elongate–oval SCT, strong to moderately developed hinge ear in LV, and nodose, massively spined, or bullate surface features.

Remarks

In the same way that the Pennyellinae constitute a distinctive blind reticulate trachyleberid-like group, so the Unicapellinae brings together an equivalent grouping that is characterized by its combination of finely reticulate often delicately foveolate surface texture with coarse spines, massive nodes, and bullae (Figs 39, 43).

Although the earliest record of the subfamily so far is of *Unicapella* in the Santonian of Zululand (personal unpublished data) its main development is in the Campanian, with the appearance of the genera *Dutoitella* in east and south-east Africa, *Atlanticythere* and *Paleoabyssocythere* in the South Atlantic basin (Benson 1977), and *Herrigocythere* in north Germany (Herrig 1965). In addition, the species described by Holden (1964) as *Idiocythere triebeli* from the Upper Campanian–Lower Maastrichtian of California may belong to *Herrigocythere*, as suggested by Gründel (1974). *Atlanticythere* and *Paleoabyssocythere* are reckoned to have lived in water depths of the order of 1 000 m (Benson 1977) and, although so far described only in detail from DSDP sites on the Rio Grande Rise (sites 356, 21 & 22), they are said to occur ‘worldwide’ (Benson 1977). *Unicapella* and *Dutoitella*, on the other hand, are thought to occur in moderate to deep continental shelf or upper slope environments in east Africa.

The northern hemisphere genera appear in the late Campanian–early Maastrichtian, whereas the southern hemisphere representatives are first found in slightly older rocks (Santonian–early Campanian). On this evidence it seems likely that the subfamily originated in the proto South Atlantic–South-western Indian Ocean area and rapidly migrated northwards.

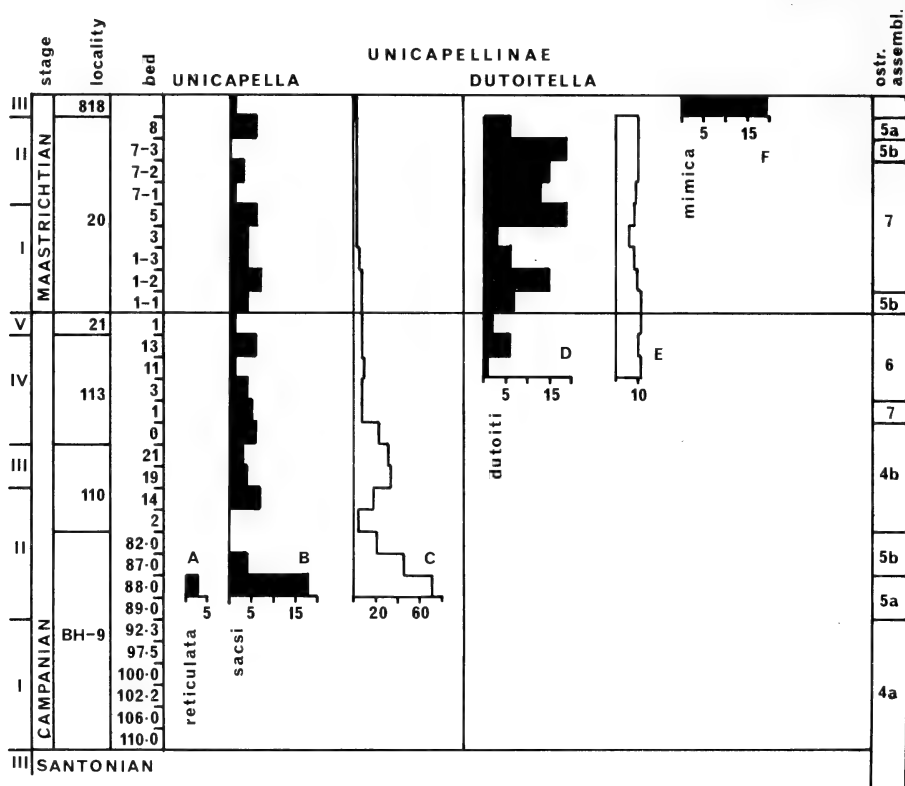


Fig. 38. Distribution of Unicapellinae in Campanian-Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Unicapella reticulata*. B. Total number of valves of *Unicapella sarsi*. C. *Unicapella sarsi* as percentage of Cytheracea. D. Total number of valves of *Dutoitella dutoiti*. E. *Dutoitella dutoiti* as percentage of Cytheracea. F. Total number of valves of *Dutoitella mimica*.

TABLE 5
Distinguishing features: *Unicapella*, *Paleoabyssocythere*, and *Herrigocythere*.

			<i>AM rim</i>	<i>SCT</i>	<i>postero-ventral bullae</i>	<i>ventro-lateral nodes</i>	<i>surface ornamentation</i>	<i>holotype length, LV mm</i>
<i>Unicapella</i>	.	.	narrow	large, dome-shaped	prominent small	small, rounded, discontinuous	foveolate to coarsely reticulate	0,55
<i>Paleoabyssocythere</i>	.		massive wide	large, elongate, with distinct posterior taper	massive	large, fused into ridge	foveolate to weakly reticulate	0,80
<i>Herrigocythere</i>	.	.	massive wide	small, elongate, posteriorly	large, rounded	indistinct, fused into ridge	smooth to foveolate	0,62

Genus *Unicapella* Dingle, 1980

Although the genus probably first appears in the Santonian of Zululand (unpublished data), *Unicapella* is typical of the Campanian–Maastrichtian, where two species are known, *U. reticulata* and *U. sacsi* (Fig. 38A–C). It is closely related to *Paleoabyssocythere* Benson, 1977, and *Herrigocythere* Gründel, 1973. All have similar surface morphologies, shell outlines and hingement (MS are so far known only for *Herrigocythere*), and generic subdivision is based primarily upon differences in the following characters: AM rim, SCT, surface ornamentation, posteroventral bulla, and ventrolateral ridge. These differences are listed in Table 5 and are sketched in Figure 39.

Unicapella reticulata Dingle, 1980

Figs 39H, 40A

Unicapella reticulata Dingle 1980: 33–34, fig. 17A–B.*Remarks*

Despite the large amount of new material studied, the only records of this distinctively ornamented species remain the three valves from sample 88.0 in the Campanian I of the Richards Bay BH–9 borehole (Dingle 1980).

Age, distribution, palaeoecology

Campanian I, Richards Bay BH–9 borehole, confined to ostracod assemblage 5a which represents a low-energy, open-water, moderate-depth environment (200–300 m, mid to outer shelf). *U. reticulata* is the only species restricted to this ecofacies.

Unicapella sacsi Dingle, 1980

Figs 37C–E, 39A, E

Unicapella sacsi Dingle, 1980: 30–32, fig. 16A–G.*Remarks*

There is some intraspecific morphological variation throughout the Zululand succession, with the Campanian II forms tending to be more coarsely reticulate and having somewhat narrower posterodorsal bullae than their younger (e.g. Maastrichtian) counterparts. In addition, the prominent LV anterodorsal ear is not always well developed in the Campanian II populations. It should be noted that the small dorsal ridge in the LV of one specimen illustrated by Dingle (1980, fig. 16B, SAM–K5611) is now considered to be an artefact caused by slight distortion of the dorsal valve edge during sedimentary compaction.

Age, distribution, palaeoecology

Campanian II–Maastrichtian II (Mfolozi, Monzi, and Nibela outcrops, Zululand and Richards Bay BH–9 borehole), Maastrichtian III (Agulhas Bank,

sample 818). This species is widely distributed throughout the Campanian–Maastrichtian rocks of south-east Africa. In Zululand, it is a consistent member of the fauna, and in the Campanian II to early Campanian IV constitutes between 10 and 70 per cent of the cytheracean element, and locally >15 per cent of the total ostracod population (Fig. 38B–C). *U. sacschi* has been found in ostracod assemblages 4b, 5a, 5b, 6–7, but is most abundant in 4b and 5, indicating that it mainly inhabited quiet, low-energy, moderate to deep-water (200–500 m) environments, probably with a preference for the mid-shelf (~200–300 m) areas (Table 4). Its presence may be particularly correlated with strong, open ocean influences.

Dutoitella gen. nov.

Derivation of name

In honour of Dr A. L. du Toit for his contributions to South African geological knowledge and his fostering of the concept of Gondwanaland.

Type species

D. dutoiti sp. nov.

Diagnosis

Non-reticulate trachyleberid with connected AM and ventrolateral ridges or clavae. The median area is occupied by a prominent nodose or dome shaped SCT and an unconnected post-adjacent node or short nodose ridge.

Remarks

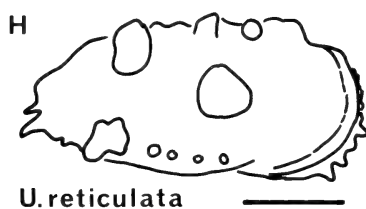
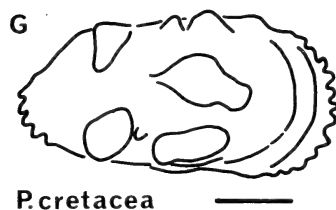
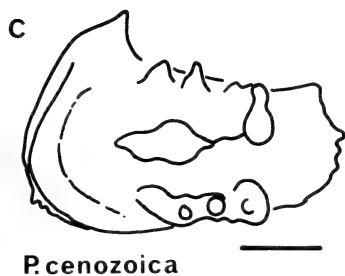
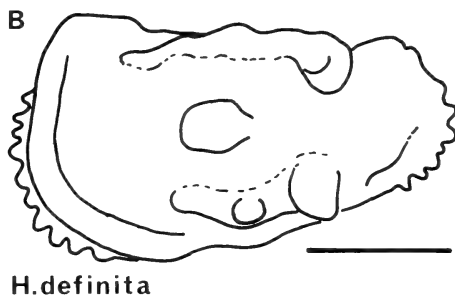
The hinge of *Dutoitella* varies from weakly hemiamphidont (*D. dutoiti*) to strongly hemiamphidont (*D. mimica*), and whilst the MS in the genotype have not been seen clearly, those of *D. mimica* show subdivided antennal and second posterior scars.

Fig. 39. Comparative morphology of various genera and species of the Unicapellinae subfam. nov. A–D. Left valves. E–H. Right valves. A. *Unicapella sacschi* Dingle, 1980, SAM-K5740, locality 20–7/1, Mfolozi River, Maastrichtian II. B. *Herrigocythere definita* (Herrig, 1965), genotype, GPIG 14/1, borehole Stubnitz 1/60 Rügen, East Germany, Lower Campanian. C. *Paleoabyssocythere cenozoica* Benson, 1977, genotype, USNM 190285, DSDP site 21A–3–4 50–56 cm, Thanetian (*Globorotalia velascoensis* Zone). D. *Paleoabyssocythere cretacea* Benson, 1977, USNM 190168, DSDP site 21–6–4 53–59 cm, Campanian (*Pseudotextularia elegans* Zone). E. *Unicapella sacschi* Dingle, 1980, genotype, SAM-K5610, BH9 88,39 m, Campanian II. F. *Herrigocythere definita* (Herrig, 1965), genotype, GPIG 14/1, borehole Stubnitz 1/60 Rügen, East Germany, Lower Campanian. G. *Paleoabyssocythere cretacea* Benson, 1977, USNM 190169, DSDP site 21–6–4 53–59 cm, Campanian (*Pseudotextularia elegans* Zone). H. *Unicapella reticulata* Dingle, 1980, SAM-K5614, BH9 88,76 m, Campanian II.

Scale bars all 200 μ .

Illustrations from following sources: A, this paper; B, Herrig (1965 fig. 1a); C, Benson (1977 pl. 2 fig. 7); D, Benson (1977 pl. 2 fig. 8); E, Dingle (1980 fig. 16A); F, Herrig (1965 fig. 1b); G, Benson (unpublished data, with permission); H, this paper.

Dutoitella is close to the early (Campanian–Maastrichtian) species of *Atlanticitythere* Benson, 1977. The two genera differ in the following points: *Atlanticitythere* does not have a continuous AM-ventrolateral ridge; the SCT and post-adjacent node or nodes are less prominent in *Atlanticitythere*; species of *Dutoitella* are significantly smaller (lengths of holotypes): *D. dutoiti* (0,57 mm), *D. mimica* (0,80 mm); *A. maestrichtia* (1,03 mm), *A. murareticulata* (0,87 mm),



A. prethalassia (0,87 mm). In addition, Benson (1977: 876–877) emphasizes the ‘almost equally rounded anterior and posterior marginal rims’ of *Atlanticythere*, whereas although this condition is almost achieved in the LV of *D. mimica*, it is not met with in the genotype or the RV of *D. mimica* (Fig. 43).

The stratigraphic and morphologic relationships between *Unicapella* and *Dutoitella* suggest that the latter evolved from the former, probably by modification of *U. sacsi* in Campanian III–IV times. The two genera have a common basic geometry and morphology, but differ in their connection or separation of the ventrolateral and AM ridges and the presence or absence of swellings post-adjacent to the SCT.

Bate (*in* Bate & Bayliss 1969) recorded the genus (as Genus C. sp.) from the middle to upper Maastrichtian of Tanzania.

Dutoitella, like its close relative *Unicapella*, is a relatively deep-water genus (outer continental shelf, possibly as deep as 500 m).

Dutoitella dutoiti sp. nov.

Figs 40B–F, 43A

Derivation of name

In honour of Dr A. L. du Toit for his pioneering contribution to geological knowledge in South Africa.

Holotype

SAM-K5742, LV, locality 20–1/2, Mfolozi River, Maastrichtian I

Paratypes

SAM-K5743, RV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5744, LV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5745, RV, locality 20–1/2, Mfolozi River, Maastrichtian I

SAM-K5746, carapace, locality 20–1/2, Mfolozi River, Maastrichtian I

Diagnosis

Species with two large, smooth, rounded median nodes.

Description

External features. In lateral view rounded AM and PM, the latter carrying stubby, posteriorly deflected spines. DM and VM straight, converging slightly posteriorly. Thick anterior marginal rim with small tubercles and spines which leads posteriorly to a thick ventrolateral ridge which probably represents five fused clavae. This ridge swings upwards posteriorly and ends at about three-quarters length. There is a short keel on the ventral surface which just protrudes beyond the VM. DM is surmounted by a weak ridge on which are situated four perforate conuli with a small posterodorsal bulla. In the RV the anterodorsal corner has a step, whereas in LV it is flaired slightly to form a small ear.

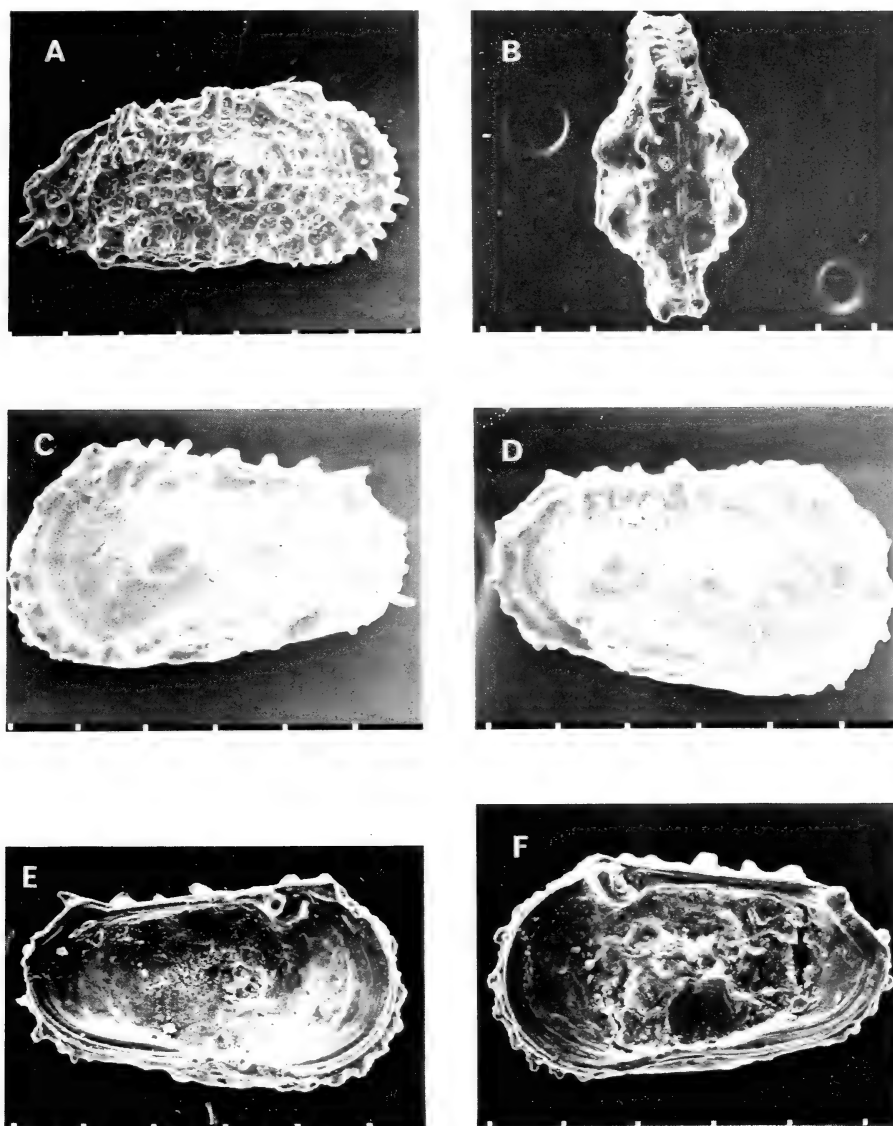


Fig. 40. A. *Unicapella reticulata* Dingle, 1980, SAM-K5614, BH9 88,76 m, RV, Campanian II. B-F. *Dutoitella dutoiti* gen. et sp. nov., locality 20-1/2, Mfolozi River, Maastrichtian I. B. SAM-K5746, dorsal view carapace. C. Holotype, SAM-K5742, LV. D. SAM-K5743, RV. E. SAM-K5744, internal LV. F. SAM-K5745, internal RV. Scale bars all 100 μ .

Medianly there is a large smooth domed SCT, and a smaller smooth domed node at about three-quarters length. In dorsal view these give a characteristic asymmetrically mammalate appearance to each valve. The surface is delicately ornamented with fine fossae that are superimposed on a faint, coarse, first-order reticulation pattern, particularly in the anterior region. There are numerous small perforate nodes on the valve surface. Ventral surface has two longitudinal ridges which frequently develop into small keels.

Internal features. Hinge amphidont, all the elements are smooth except PTE which is rounded and weakly subdivided. There is a narrow, terminally widening groove immediately above the hinge in RV. MS not seen. MA moderately wide, no vestibule. MPC fine, slightly sinuous: fifteen anteriorly, ten posteriorly.

Remarks

D. dutoiti differs from *D. mimica* in possessing a node rather than a ridge post-adjacent to SCT, and in having a continuous ridge rather than a nodose lineament ventrolaterally (Fig. 43).

Dimensions (mm)

	length	height	width
K5742	0,57	0,33	
K5743	0,55	0,32	
K5744	0,54	0,30	
K5745	0,53	0,29	
K5746	0,54		0,28
Other material	0,58	0,34	
Other material	0,57	0,30	

Age, distribution, palaeoecology

Campanian IV to Maastrichtian II (Monzi, Mfolozi and Nibela areas Zululand) (Fig. 38D–E). This species is consistently present in small numbers (2–3% total population, 8–11% total cytheraceans) throughout its range, and because it has been found evenly distributed in ostracod assemblages 5a, 5b, 6–7, it has been selected as a zonal marker for the upper part of the succession in south-east Africa. The even distribution of *D. dutoiti* through the mid shelf (?200 m) to deep water (?outer shelf/upper slope, >500 m) sedimentary environments indicates that it is not as environmentally bound as its relative *U. sacsi*, which becomes relatively scarce in the deep-water facies. It is replaced in the Maastrichtian III by *D. mimica*.

Dutoitella mimica sp. nov.

Figs 37F, 41A–F, 42A–B, 43B, F, 44B

Genus C. sp. Bate, 1969 (in Bate & Bayliss 1969): 143, pl. 7 (fig. 15).

Trachyleberis schizospinosa Dingle 1971: 406–408, fig. 10. (Some of the paratypes designated MG–4–1–4 belong to *D. mimica*.)

Derivation of name

Latin *mimicus* (counterfeit): reference to similarity with *Atlanticythere maestrichtia* Benson, 1977.

Holotype

SAM-K5747, LV, sample 818, Agulhas Bank, Maastrichtian III

Paratypes

SAM-K5748, RV, sample 818, Agulhas Bank, Maastrichtian III

SAM-K5749, LV, sample 818, Agulhas Bank, Maastrichtian III

SAM-K5750, RV, sample 818, Agulhas Bank, Maastrichtian III

SAM-K5751, LV, sample 818, Agulhas Bank, Maastrichtian III

SAM-K5752, LV, JC-1 borehole, 1 811 m, Maastrichtian

Diagnosis

Species with nodose SCT, and three perforated nodes sub-adjacent to it.

Description

External features. AM broadly rounded with spinose and nodose rim. PM and LV broadly rounded, in RV asymmetric and slightly acuminate, ventrally spinose and nodose in both valves. DM straight with numerous short spines, and a distinct step at the anterior cardinal angle in RV. VM slightly convex, more so in the RV, the outline is partly obscured by a short keel on the ventral surface. Lateral surface smooth or foveolate with fine ridges forming a loose network in the central part of the valve and a first-order reticulation in the anterior area. The dorsal area has a poorly developed lineament of stout, perforated spines, several of which in the LV are deflected posteriorly. They form a weak bulla at the posterior cardinal angle. There is an upward deflected ventrolateral line of stout, perforate nodes which is continuous with the AM rim. The SCT is prominent, domed and nodose and there is a short ridge of three perforate nodes post-adjacent but not connected to it.

Internal features. Hinge hemiamphidont with fist-like PTE in RV. MS consist of two rounded anterior scars and a vertical row of elongate adductors, the second of which is subdivided. MA fairly narrow with small anterior and posterior vestibules. Up to eighteen thin, straight anterior MPC; seven to ten short, straight posterior MPC.

Remarks

Dingle (1971) included representatives of this species in his population of *Trachyleberis schizospinosa*. They can be separated from it on the basis of valve outline and surface ornamentation. *D. mimica* differs from *D. dutoiti* in the morphology of the posteromedian elevation and ventrolateral ridge (Fig. 43). Surface nodes on the specimens from JC-1 borehole are slightly more massive than those from the Agulhas Bank, although this may in part be due to slight abrasion.

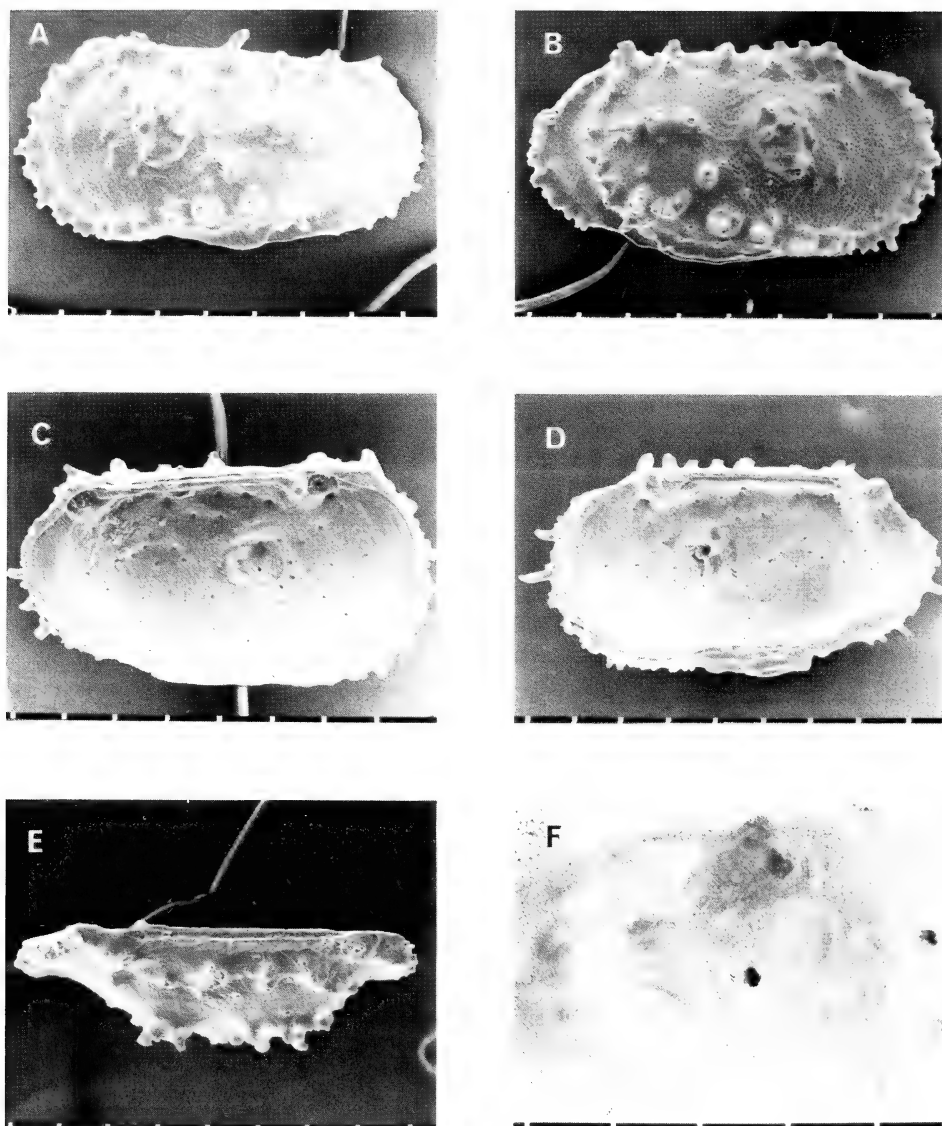


Fig. 41. *Dutoitella mimica* gen. et sp. nov. TBD 818 Alphard Formation, Agulhas Bank, Maastrichtian III. A. Holotype, SAM-K5747, LV. B. SAM-K5748, RV. C. SAM-K5749, internal LV. D. SAM-K5750, internal RV. E. SAM-K5751, dorsal view LV. F. SAM-K5749, MS LV.

Scale bars: F = 30µ, others = 100µ.

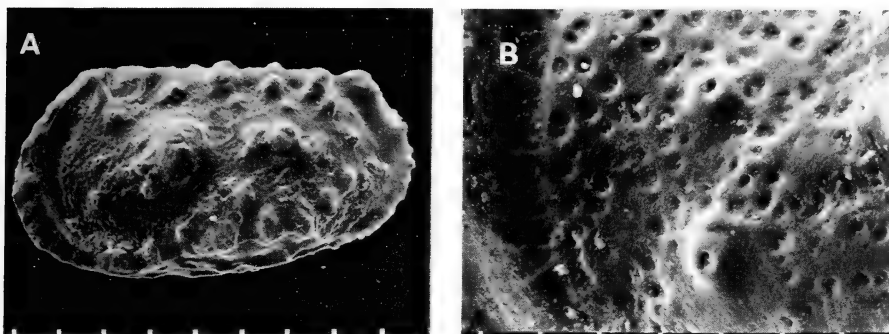


Fig. 42. *Dutoitella mimica* gen. et sp. nov., SAM-K5752, JC-1 1811 m, LV, Maastrichtian.
A. Lateral view. B. Detail anterior area.
Scale bars: A = 100 μ , B = 30 μ .

D. mimica superficially resembles *Atlanticythere maestrichtia* Benson, 1977, but differs in the essential genetic characters (see remarks and designation of *Dutoitella*).

Bate (*in* Bate & Bayliss 1969) recorded one valve of *D. mimica* (his Genus C. sp.) from the Upper Cretaceous of Tanzania (1969, pl. 7 (fig. 15)) but there is some confusion in his text as to the exact locality and age of the specimen. One page 123 it is stated to have been found in the upper Campanian, but on page 143, and according to the sample number (BM 108) it is said to be mid-upper Maastrichtian. The latter will be assumed here because on fig. 7 sample 168 is clearly shown as Maastrichtian.

Dimensions (mm)

	length	height	width
K5747	0,81	0,41	
K5748	0,80	0,42	
K5749	0,78	0,44	
K5750	0,80	0,43	
K5751	0,78		0,20
K5752	0,88	0,46	

Age, distribution, palaeoecology

Maastrichtian III (sample 818, Agulhas Bank), late Campanian to lower Maastrichtian (1 871–1 811 m), JC-1 borehole, and Maastrichtian (Tanzania). The Agulhas Bank sedimentary environment is thought to represent an unusual setting: a quiet, shallow-water environment on the outer edge of the continental shelf or the uppermost continental slope. It is an important member of this population, constituting 10 per cent of the total fauna. In the JC-1 borehole, *D. mimica* occurs at level 1811 (Maastrichtian) with *Bythocypris?* and *Cytherella* sp., and at level 1871 (Campanian) on its own.

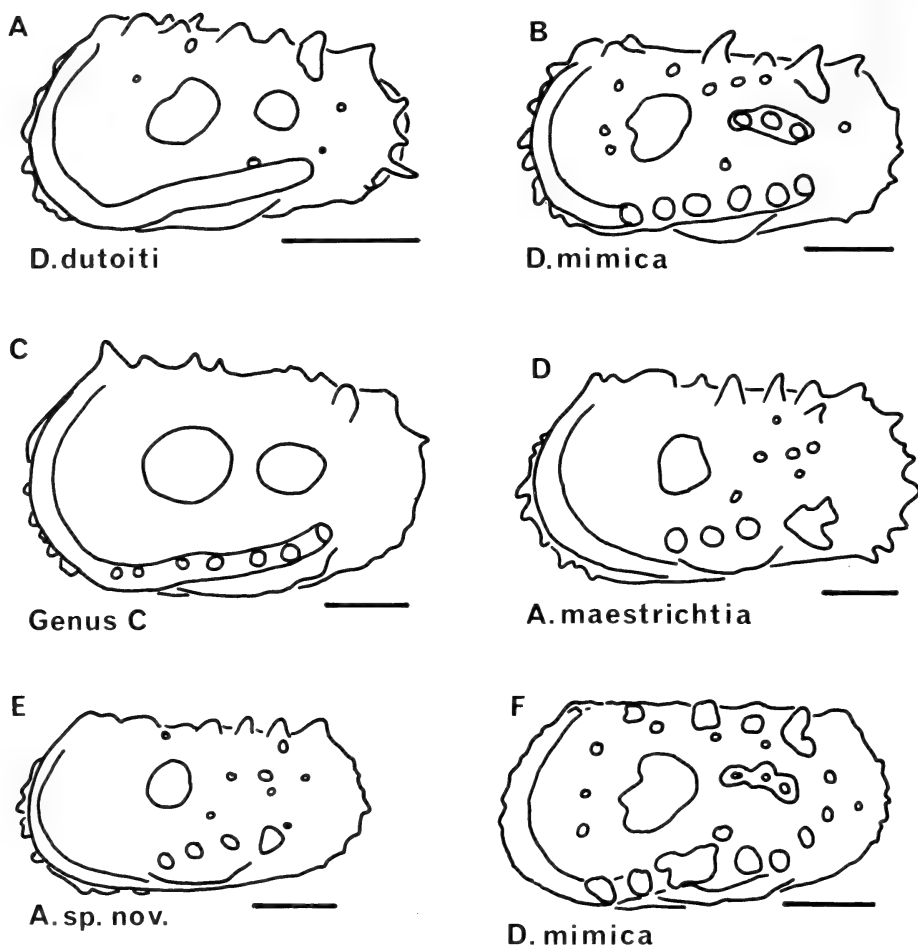


Fig. 43. Comparative morphology of various genera and species of the Unicapellinae subfam. nov. All left valves. A. *Dutoitella dutoiti* gen. et sp. nov., genotype, SAM-K5742, locality 20-1/2, Mfolozi River, Maastrichtian I. B. *Dutoitella mimica* gen. et sp. nov., SAM-K5747, TBD 818 Alphard Formation Agulhas Bank, Maastrichtian III. C. Genus C Bate, 1969 = *Dutoitella mimica*, BM Io. 1304, sample BM168 Kilwa area Tanzania, Maastrichtian. D. *Atlanticythere maestrichtia* Benson, 1977, genotype, USNM 190166, DSDP site 21-4-4 60-66 cm, Maastrichtian (top *Rugotruncana subcircumnoidifera* Zone). E. *Atlanticythere* sp. nov. USNM 190755, DSDP site 21-7-4 53-59 cm, Campanian. F. *Dutoitella mimica* gen. et sp. nov., SAM-K5752, JC-1 1811 m Maastrichtian.

Scale bars all 200 μ .

Illustrations from following sources: A, this paper; B, this paper; C, Bate & Bayliss (1969 pl. 7 fig. 15); D, Benson (1977 pl. 2 fig. 4); E, Benson (unpublished data, with permission); F, this paper.

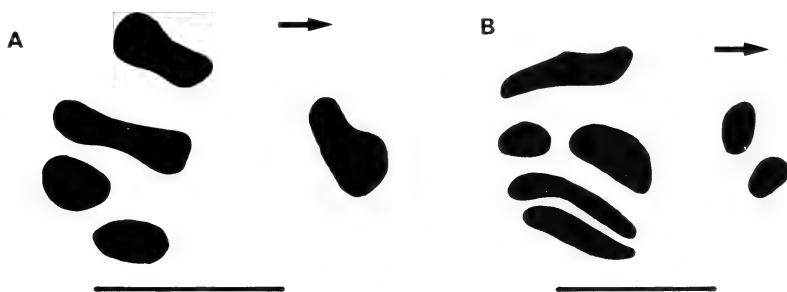


Fig. 44. Muscle scars. A. *Agulhasina quadrata* Dingle, 1971, TBD 818 Alphard Formation, Agulhas Bank, LV, Maastrichtian III. B. *Dutoitella mimica* gen. et sp. nov. SAM-K5749, TBD 818 Alphard Formation, Agulhas Bank, LV, Maastrichtian III. Scale bars 60 μ .

Subfamily **Trachyleberidinae** Sylvester-Bradley, 1948

This subfamily is well represented by twenty-two species in the Campanian–Maastrichtian rocks of south-east Africa, with the genera *Haughtonileberis*, *Oertliella*, *Trachyleberis*, and *Hermanites* particularly important.

Genus *Haughtonileberis* Dingle, 1969

This genus is one of the most important of the Cytheracea taxa in the Upper Cretaceous in south-east Africa. Its earliest records in this area are from the Santonian, and Dingle (1976) has reported one species in the Eocene, but recently Grosdidier (1979) has tentatively assigned several species to it from the Cenomanian–Turonian of Gabon.

For most of the Campanian–Maastrichtian period in south-east Africa, the genus had numerically passed its peak, although during the Campanian I it is represented by four species (Fig. 45): *H. haughtoni*, *H. fissilis*, *H. vanhoepeni*, and *H. nibelaensis*. Only *H. nibelaensis* is confined to strata of Campanian–Maastrichtian age, and only *H. fissilis* ranges up into the Maastrichtian. Numerically, the genus is most important in the Santonian (Dingle 1980) where it locally reaches over 50 per cent of the total ostracod populations in two species (*H. haughtoni* and *H. fissilis*). There is a steady, if erratic, decline in numbers through the upper Santonian, so that, although a further species appears in the uppermost Santonian (*H. vanhoepeni*), the Campanian opens with the genus constituting about 20 per cent of the total ostracod population (Fig. 45E). This abundance is maintained throughout Campanian I, where *H. vanhoepeni* reaches its local acme (5–8%), but a rapid decline occurs across the Campanian I–II boundary (to about 6%) and despite a temporary resurgence at the top of Campanian II (~20%) where *H. nibelaensis* temporarily becomes important, the genus is represented in small numbers by only two species in rocks younger than Campanian II. Although ecological factors must have played a role in this decline, the fact that both *H. haughtoni* and *H. fissilis* show considerable environmental tolerance in the Santonian (Dingle 1980) suggests that their

decline at the end of Campanian I was to a large extent a phylogenetic phenomenon.

The genus is represented in the Maastrichtian by one record only: two specimens of *H. fissilis* at locality 20 (Mfolozi River), but the closeness of *H. radiatus* (Eocene, borehole JC-1, Dingle 1976) to *H. fissilis* indicates that the latter species, or a development of it, survived locally through the rest of Maastrichtian and Palaeocene times.

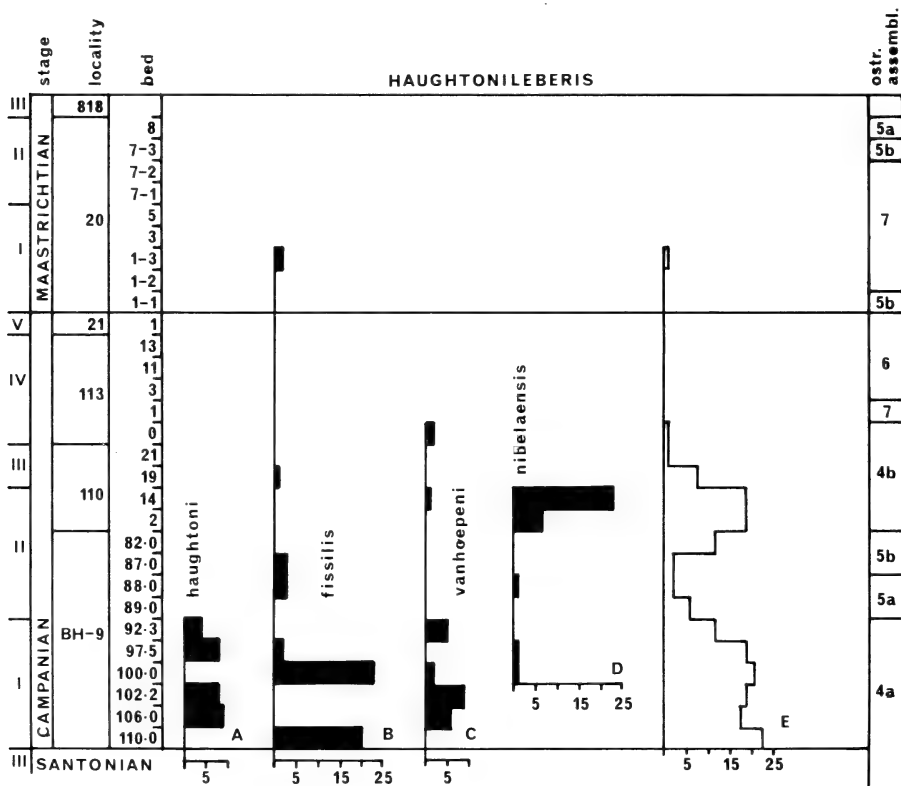


Fig. 45. Distribution of *Haughtonileberis* in Campanian-Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *H. haughtoni*. B. Total number of valves of *H. fissilis*. C. Total number of valves of *H. vanhoepeni*. D. Total number of valves of *H. nibelaensis*. E. *Haughtonileberis* as percentage of total ostracod population.

Haughtonileberis haughtoni Dingle, 1969

Fig. 48E

Haughtonileberis haughtoni Dingle, 1969: 372-373, fig. 15; 1980: 39, fig. 21A-E.

Remarks

Of the two morphotypes recognized by Dingle (1980), only the elongate form occurs in the Campanian I section of the Richards Bay BH-9 borehole.

Here the species is at the top of its range, and occurs in only small numbers compared to its importance in the Santonian strata.

Age, distribution, palaeoecology

Santonian II to Campanian I (Umzamba and Richards Bay BH-9 borehole). *H. haughtoni* is an environmentally tolerant species, having been recorded from ostracod assemblages 1-3, and 4a (Dingle 1980). It is most abundant in assemblage 2 and preferred shallow-water (<100 m), low-energy environments with a restricted access to the open ocean (Table 4).

Haughtonileberis fissilis Dingle, 1969

Fig. 48F

Haughtonileberis fissilis Dingle, 1969: 374-375, fig. 16; 1976: 59, fig. 3(48); 1980: 39, fig. 22A-B.

Remarks

Of the two morphotypes recognized by Dingle (1980), only the more coarsely reticulate variety occurs in the Campanian-Maastrichtian strata.

Age, distribution, palaeoecology

Santonian II to Maastrichtian II (Umzamba, and Richards Bay BH-9 borehole and Mfolozi and Nibela outcrops, Zululand). Although *H. fissilis* has been found in ostracod assemblages 1-3, 4a, 4b, 5a, 5b, and 7, and is obviously an environmentally tolerant species, it is found in relatively large numbers only in assemblage 4a. On this evidence the species preferred low-energy, moderate-depth (?100-200 m inner-mid shelf), open-water environments, suggesting that it inhabited deeper and less-restricted areas than its close relative *H. haughtoni* (Table 4).

Haughtonileberis vanhoepeni Dingle, 1980

Fig. 46A

Haughtonileberis vanhoepeni Dingle, 1980: 42-44, figs 22H, 23A-F.

Remarks

No important morphological variations have been recognized in this species throughout its short range.

Age, distribution, palaeoecology

Uppermost Santonian III to Campanian IV (Richards Bay BH-9 borehole and Nibela Peninsula). Although two specimens have been found in assemblage 3, *H. vanhoepeni* is to all intents and purposes environmentally bound to assemblage 4, with a clear preference for the conditions represented by sub-assemblage 4a: low-energy, moderate-depth (?100-200 m inner-mid shelf), open-water environments (Table 4).

Haughtonileberis nibelaensis sp. nov.

Fig. 46B-F

Derivation of name

Locality of type.

Holotype

SAM-K5754, LV, locality 110-14, Nibela, Campanian II

Paratypes

SAM-K5755, RV, locality 110-14, Nibela, Campanian II

SAM-K5756, LV, locality 110-14, Nibela, Campanian II

SAM-K5757, RV, locality 110-14, Nibela, Campanian II

SAM-K5758, carapace, locality 110-14, Nibela, Campanian II

Diagnosis

Heavily calcified species with intercostal ornamentation that ranges from coarsely reticulate to almost smooth. Anterior cardinal angle is prominently rounded and the ventrolateral ridge is looped.

Description

Moderately large, heavily calcified species.

External features. In lateral view, AM is broadly rounded, with a somewhat flaired appearance, PM is triangular in outline, DM and VM straight, posteriorly tapering. Highest point over anterior cardinal angle, widest point in dorsal view over SCT. Ornamentation is dominated by three narrow, sharp, longitudinal ridges. The dorsal ridge is the shortest and is slightly convex, obscuring the dorsal margin: the median ridge crosses a subdued SCT and typically splits anteriorly: the ventral ridge forms a loop that widens posteriorly. A large rounded eye spot lies on a short anterodorsal ridge that extends most of the way round the anterior margin. Surface ornamentation within the species varies from coarsely reticulate to almost smooth with ghost reticulation and small prominent pustules.

Internal features. Hinge amphidont with weakly subdivided terminal elements in the RV. The RV ATE has a prominent anterior shoulder which fits into a small socket in the LV. ME is smooth. MA moderately wide, up to twenty-five long, fine anterior MPC, up to fifteen posterior MPC. MS consist of a hooked (sometimes almost subdivided) anterior scar and four elongate adductors, all lying in a shallow pit.

Remarks

This species is closest to *H. fissilis* with its split median rib, but has a more symmetrical anterior outline, a more triangular posterior outline and a looped ventrolateral ridge. *H. nibelaensis* is similar in lateral outline to *H. vanhoepeni* but the latter has a different rib disposition and is a smaller species.

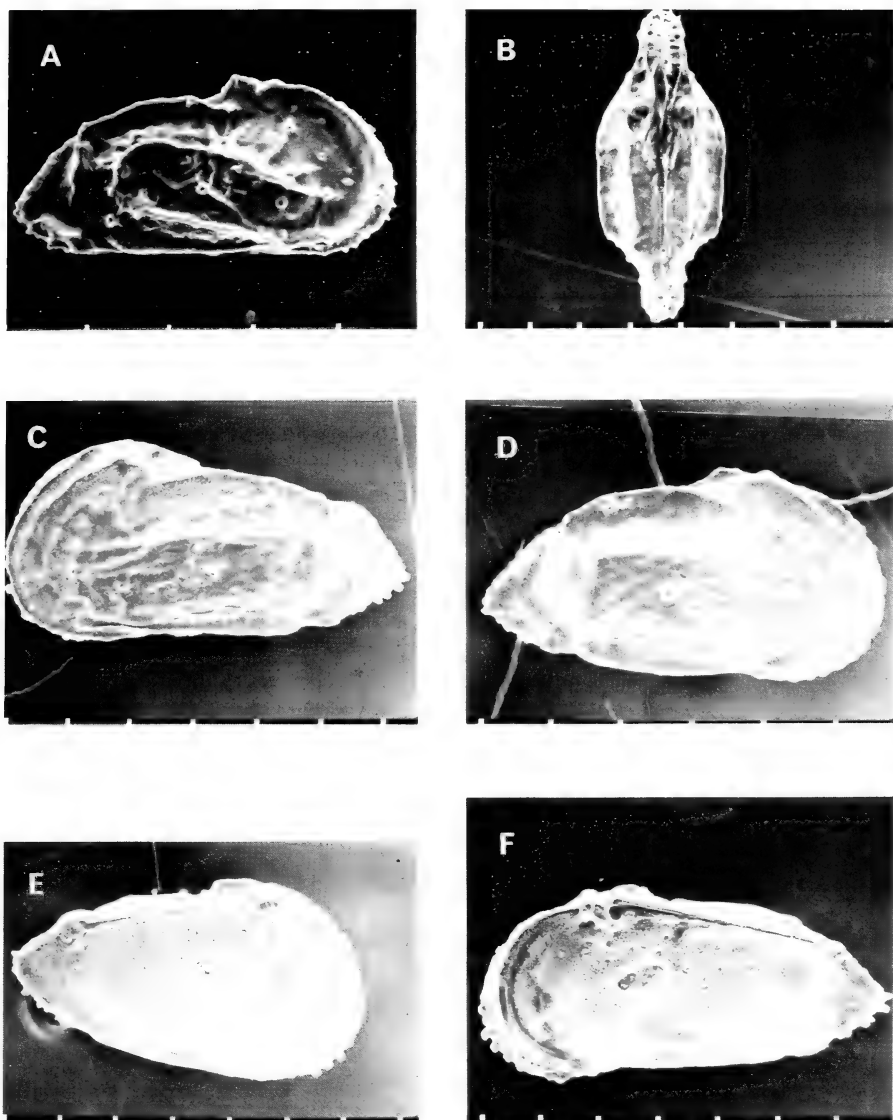


Fig. 46. A. *Haughtonileberis vanhoepeni*, SAM-K5632, BH9 100,0 m, RV, Campanian I. B-F. *Haughtonileberis nibelaensis* sp. nov., locality 110-14, Nibela Peninsula, Campanian II. B. SAM-K5758, dorsal view carapace. C. Holotype, SAM-K5754, LV. D. SAM-K5755, RV. E. SAM-K5756, internal LV. F. SAM-K5757, internal RV.

Scale bars all 100 μ .

Dimensions (mm)

	length	height	width
K5754	0,65	0,31	
K5755	0,58	0,30	
K5756	0,62	0,34	
K5757	0,67	0,32	
K5758	0,62		0,25
Other material	0,65	0,31	
Other material	0,72	0,30	
Other material	0,61	0,32	
Other material	0,57		0,25

Age, distribution, palaeoecology

Campanian I to Campanian II (Richards Bay BH-9 borehole and Nibela Peninsula). Although *H. nibelaensis* occurs in assemblages 4a, 4b, and 5a (Fig. 45D) it has a strong preference for 4b, indicating that it is to all intents and purposes environmentally bound to conditions of low energy, moderate depth (?200 m inner-mid shelf) with open-water connections. *H. nibelaensis* has the deepest water preference of all the known species of the genus (Table 4).

Genus *Oertliella* Pokorný, 1964

This genus occurs sporadically in the late Cretaceous of south-east Africa, and is numerically important (10–20% of total cytheraceans) in Campanian I and II and Maastrichtian I and II strata (Fig. 47E). It is represented by four species: *O. pennata*, *O. sp. A*, *O. africana*, and *O. maastrichtia* of which the last two are confined to Campanian–Maastrichtian, and the first two to Santonian–Campanian strata.

Oertliella pennata Dingle, 1980

Fig. 48A

Acanthocythereis? aff. *A. horridula* (Bosquet, 1854), Dingle, 1969: 378–380, fig. 19.
Oertliella pennata Dingle 1980: 46–49, fig. 26A–E.

Remarks

No additional material is available for this species beyond that already recorded by Dingle (1980).

Age, distribution, palaeoecology

Santonian III to Campanian II (Richards Bay BH-9 borehole), Santonian III (bed Pi 3) (Umzamba). Two valves of *O. pennata* were found in ostracod assemblage 2, but the species is consistently present only in assemblages 3, 4a, and 5a, with a maximum in 4a indicating a preference for low-energy, moderate-depth (?100–200 m, inner-mid shelf) open-water conditions (Fig. 47A, Table 4). Because of its apparent tolerance over various environments in the inner to mid shelf locations, the disappearance of *O. pennata* during Campanian II times is probably phylogenetically significant.

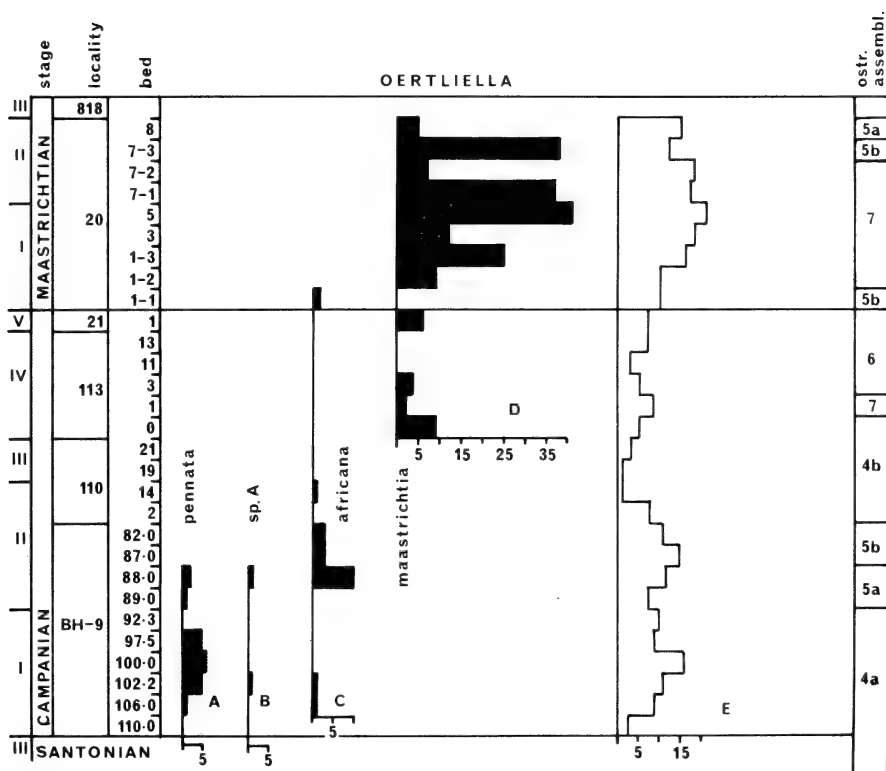


Fig. 47. Distribution of *Oertliella* in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *O. pennata*. B. Total number of valves of *O. sp. A*. C. Total number of valves of *O. africana*. D. Total number of valves of *O. maastrichtia*. E. *Oertliella* as percentage of Cytheracea.

Oertliella sp. A

Fig. 48B

Oertliella sp. A Dingle, 1980: 50–52, fig. 26F.

Remarks

Three valves of this species were recorded by Dingle (1980) in the Richards Bay BH-9 borehole. No additional specimens have come to light, so their taxonomic position remains uncertain.

Age, distribution, palaeoecology

Santonian III to Campanian II (Richards Bay BH-9 borehole). Too few valves are available for an assessment of the species' palaeoenvironmental preferences, though it appears to be confined to moderate-water depth (Fig. 47B, Table 4).

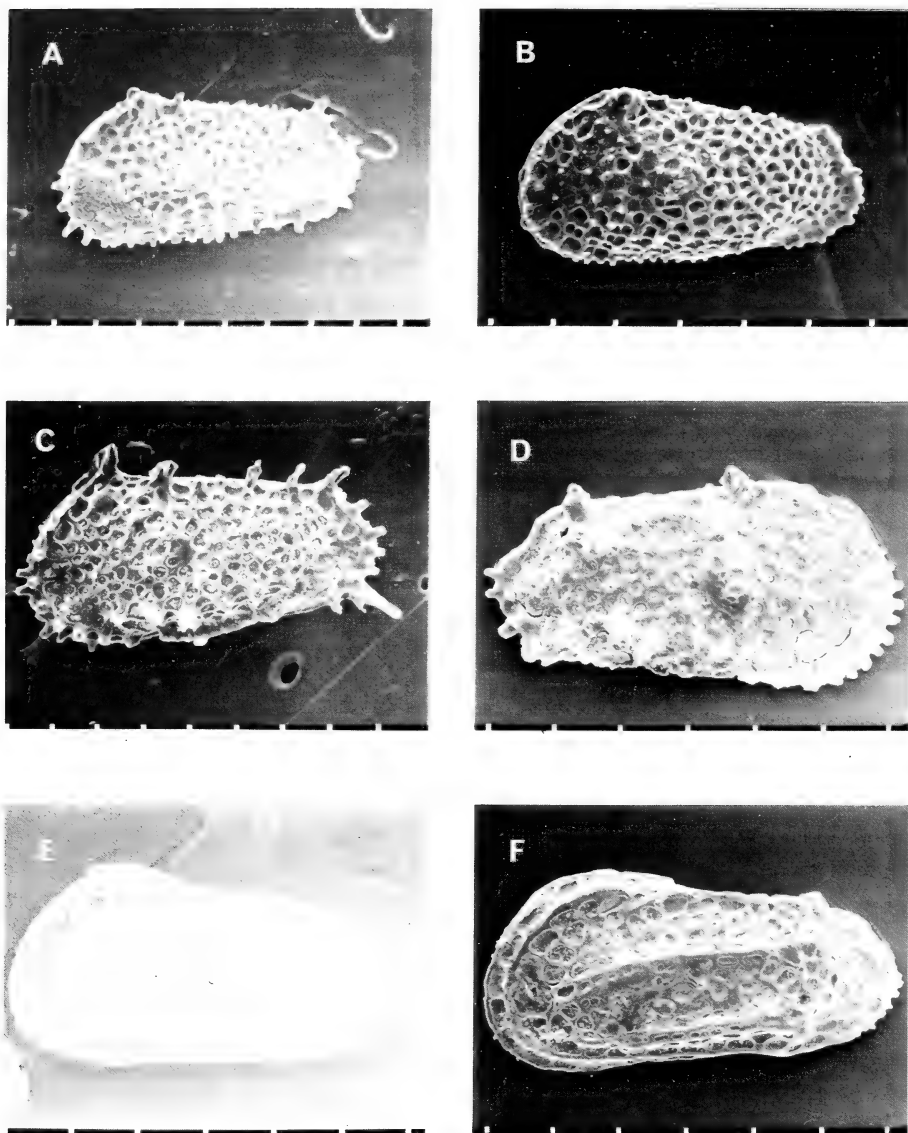


Fig. 48. A-D. *Oertliella*. A. *O. pennata* Dingle, 1980, SAM-K5759, BH9 102,6 m, LV, Campanian I. B. *O. sp. A*, SAM-K5760, BH9 106,0 m, LV, Campanian I. C. *O. africana* Dingle, 1980, SAM-K5648, BH9 82,03 m, LV, Campanian II. D. *O. africana*, SAM-K5761, locality 20-1/1, Mfolozi River, RV, Maastrichtian I. E. *Haughtonileberis haughtoni* Dingle, 1969, SAM-K5627, BH9 92,27 m, LV, Campanian I. F. *Haughtonileberis fissilis* Dingle, 1969, SAM-K5762, locality 20-1/3, Mfolozi River, LV, Maastrichtian I.

Scale bars all 100 μ .

Oertliella africana Dingle, 1980

Fig. 48C–D

Oertliella africana Dingle, 1980: 49–50, figs 26G, 27A–E.*Remarks*

Two specimens closely comparable to the lower Campanian material from the Richards Bay BH–9 borehole (Dingle 1980) have been found at locality 20 (Mfolozi River) in Maastrichtian I sediments. They differ only in possessing a double-bladed spine post-adjacent to the weak eye spot, a somewhat more inflated ventral outline and an additional spine immediately below the postero-dorsal margin spine (compare C and D in Fig. 48). In addition they are slightly smaller than the types described by Dingle (1980).

Dimensions (mm)

	length	height
K5761	0,61	0,31
Other material	0,59	0,33

Mean of four specimens quoted by Dingle (1980) from the BH–9 borehole: length 0,73 mm and height 0,34 mm.

Age, distribution, palaeoecology

Accepting that the two specimens mentioned above fall within the definition of the species, *O. africana* ranges Campanian I to Maastrichtian I (Richards Bay BH–9 borehole, and Mfolozi and Nibela outcrops) (Fig. 47C). It has been found in ostracod assemblages 4a, and 5a, 5b, and it is significant that the Maastrichtian occurrence is in assemblages assigned to 5b. It seems likely that this species' preference is for the environments represented by assemblage 5a, viz: low-energy, open-water, moderate-depth (?200–300 mid-outer shelf) environments. On this evidence it occupied slightly deeper-water conditions than *O. pennata* (Table 4).

Oertliella maastrichtia sp. nov.

Fig. 49A–E

Derivation of name

Age of largest populations.

Holotype

SAM–K5763, LV, locality 20–7/1, Mfolozi River, Maastrichtian II

Paratypes

SAM–K5764, RV, locality 20–7/1, Mfolozi River, Maastrichtian II

SAM–K5765, LV, locality 20–7/1, Mfolozi River, Maastrichtian II

SAM–K5766, RV, locality 20–7/1, Mfolozi River, Maastrichtian II

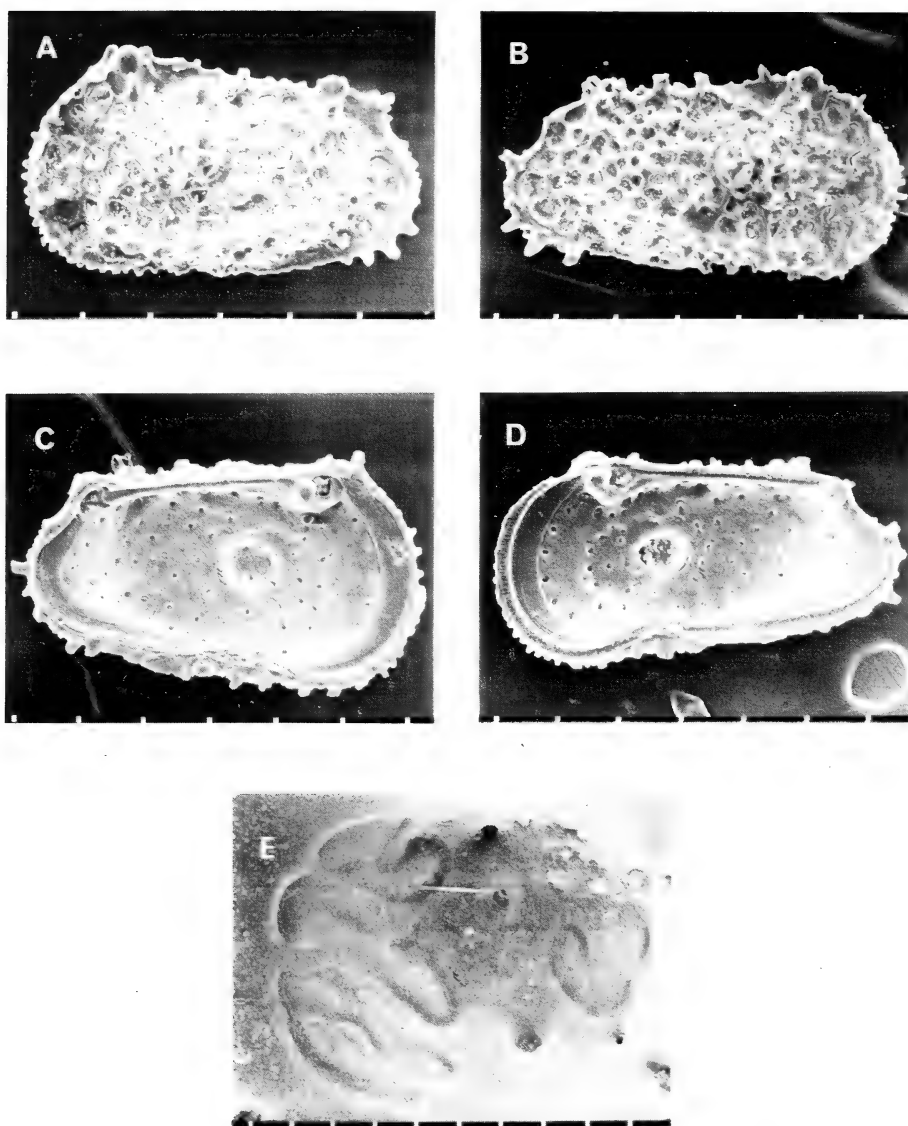


Fig. 49. *Oertliella maastrichtia* sp. nov., locality 20-7/1, Mfolozi River, Maastrichtian II.
A. Holotype, SAM-K5763, LV, B. SAM-K5764, RV. C. SAM-K5765, internal LV.
D. SAM-K5766, internal RV. E. SAM-K5765, MS LV.
Scale bars: E = 10 μ , others = 100 μ .

Diagnosis

Species with large turreted eye spot and pennate spine at posterior end of dorsal ridge.

Description

External features. In lateral view quadrate. Symmetrically rounded, spinose AM. Slightly acuminate, spinose PM, with pronounced posterodorsal concavity. DM straight, VM gently convex. Surface strongly reticulate with numerous conjunctive spines, and occasional normal pore openings within fossae. Narrow, well-developed anterior marginal rim with numerous stubby spines. There is a well-developed ventrolateral ridge which is upcurved at its anterior and posterior ends, and is surmounted by numerous large spines. The dorsal ridge is short, set away from the margin and carries three spines which lie anterior of a large pennate bulla at the posterior termination. There is a prominent spinose SCT, and the eye spot is large, spherical, and perched prominently at the anterior cardinal angle on a spinose turret.

Internal features. Hinge amphidont with the RV PTE distinctly subdivided; other elements are smooth. MA narrow, no vestibule. MPC straight: seventeen anteriorly, seven posteriorly. MS lie in a deep sub-central pit and consist of four ovate adductors, the middle two being particularly elongate, and a V-shaped anterior scar. The top adductor is dorsally indented.

Remarks

O. maastrichtia is very close to *O. exquisita* Bate from the Campanian of Western Australia. The new species differs on the following points: it is somewhat more elongate, and has a distinct posterodorsal concavity which *O. exquisita* lacks; the adductor MS of the two species are different in shape; the RV PTE of *O. maastrichtia* is clearly subdivided whereas it is only weakly so in the Australian form; *O. exquisita* lacks the pennate spine at the posterior end of the dorsolateral ridge. Although *O. exquisita* has not been proven from Maastrichtian strata, it is possible that the two species have very similar time ranges. Within the South African context, it appears that *O. maastrichtia* evolved from *O. pennata* (Santonian–Campanian) by a process of ornament modification and slight changes in outline. It is an important element of the cytheracean population (>10%, up to 20%) in Maastrichtian times, and locally constitutes 10 per cent of the total ostracod fauna.

Dimensions (mm)

	length	height
K5763	0,58	0,33
K5764	0,65	0,34
K5765	0,61	0,34
K5766	0,66	0,35
Other material	0,64	0,36
Other material	0,65	0,36
Other material	0,65	0,34

Age, distribution, palaeoecology

Campanian IV to Maastrichtian II (Monzi, Mfolozi and Nibela outcrops, Zululand) (Fig. 47D). *O. maastrichtia* occurs in ostracod assemblages 4b, 5a, 5b, 6–7, with a clear preference for the conditions represented by 7, viz.: deep (>500 m, outer shelf/upper continental slope), oceanographically stable environments. It therefore inhabited distinctly deeper water than *O. africana* (Table 4).

Genus *Hermanites* Puri, 1955

This genus is represented by two species (*H. kennedyi*, *H? arcus*), in the Campanian–Maastrichtian strata of south-east Africa, one of which (*H. kennedyi*), for much of its range, constitutes an important element of the ostracod fauna: 8–10 per cent total population, and 30–40 per cent cytheracean population (Fig. 50). Both species appear to have favoured moderate to deep water environments.

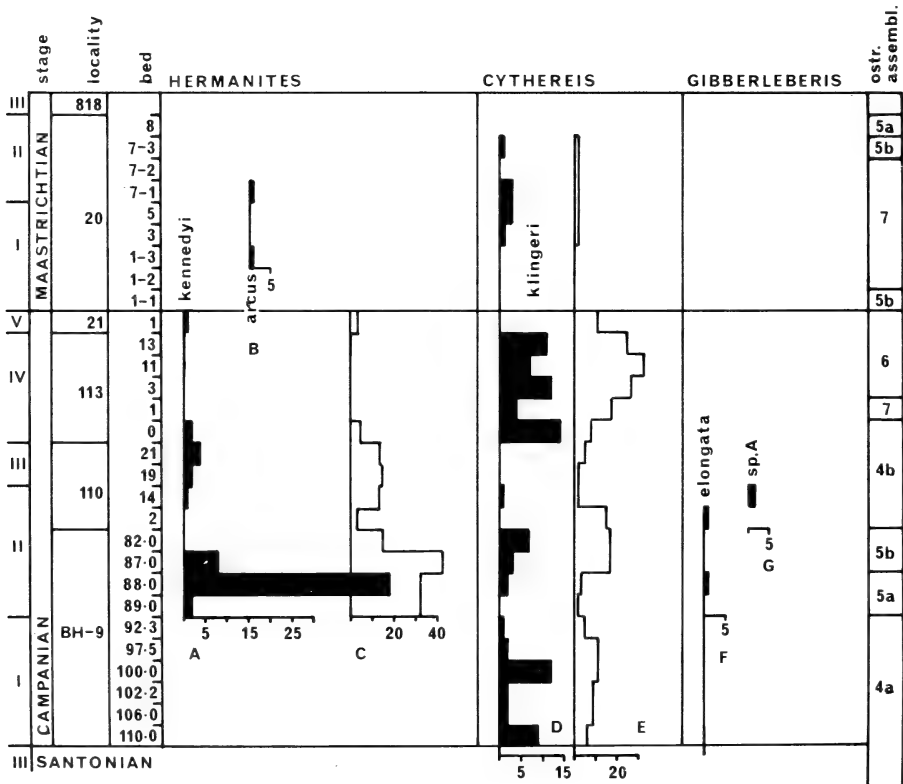


Fig. 50. Distribution of *Hermanites*, *Cythereis*, and *Gibberleberis* in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Hermanites kennedyi*. B. Total number of valves of *Hermanites? arcus*. C. *Hermanites kennedyi* as percentage of Cytheracea. D. Total number of valves of *Cythereis klinger*. E. *Cythereis klinger* as percentage of Cytheracea. F. Total number of valves of *Gibberleberis elongata*. G. Total number of valves of *Gibberleberis* sp. A.

Hermanites kennedyi Dingle, 1980

Fig. 51A–B

Hermanites kennedyi Dingle, 1980: 44–46, figs 22C–G, 24A–F.**Remarks**

H. kennedyi is a distinctive, relatively environmentally tolerant, and locally abundant species. For this reason it has been selected as a zonal fossil for the ostracod zonation scheme proposed herein. The specimens that occur in the Richards Bay BH–9 borehole and at outcrops in Zululand show no significant morphological variations throughout the species' range, but the representatives from Igoda tend to be slightly less coarsely reticulate (particularly the SCT) and have less flared dorsal and ventral ridges. These specimens are, however, worn and have considerable secondary crystalline calcite overgrowth which might have reduced the angularity of the positive surface features.

Age, distribution, palaeoecology

Campanian II to Campanian V (Richards Bay BH–9 borehole, and Monzi and Nibela Peninsula, Zululand), late Campanian/early Maastrichtian (Igoda). *H. kennedyi* is a member of ostracod assemblages 4b, 5a, 5b, and 6 with a strong preference for assemblage 5 (both a and b) where it locally forms between 30 and 40 per cent of the cytheracean element (Fig. 50A, C, Table 4). On this evidence it evidently preferred low-energy, moderate-depth (?200–300 m, mid-outer shelf) environments.

At Igoda, *H. kennedyi* is a minor element of the ostracod population (4%) and is relatively unimportant (7%) within the cytheraceans, suggesting that it was not in a preferred environment during the deposition of the Igoda assemblage.

Hermanites? arcus sp. nov.

Fig. 51C

Derivation of name

Latin *arcus* (bow): reference to bow-shaped combination of dorsal and median lateral ridges.

Holotype

SAM–K5768, RV, locality 20–1/3, Mfolozi River, Maastrichtian I.

Diagnosis

Species with bow-shaped combination of dorsal and median lateral ridges.

Description

External features. In lateral view, elongate with broadly rounded and weakly spinose AM, asymmetrically acuminate PM that is deflected ventrally and bears spines posteroventrally. DM and VM straight, converging slightly

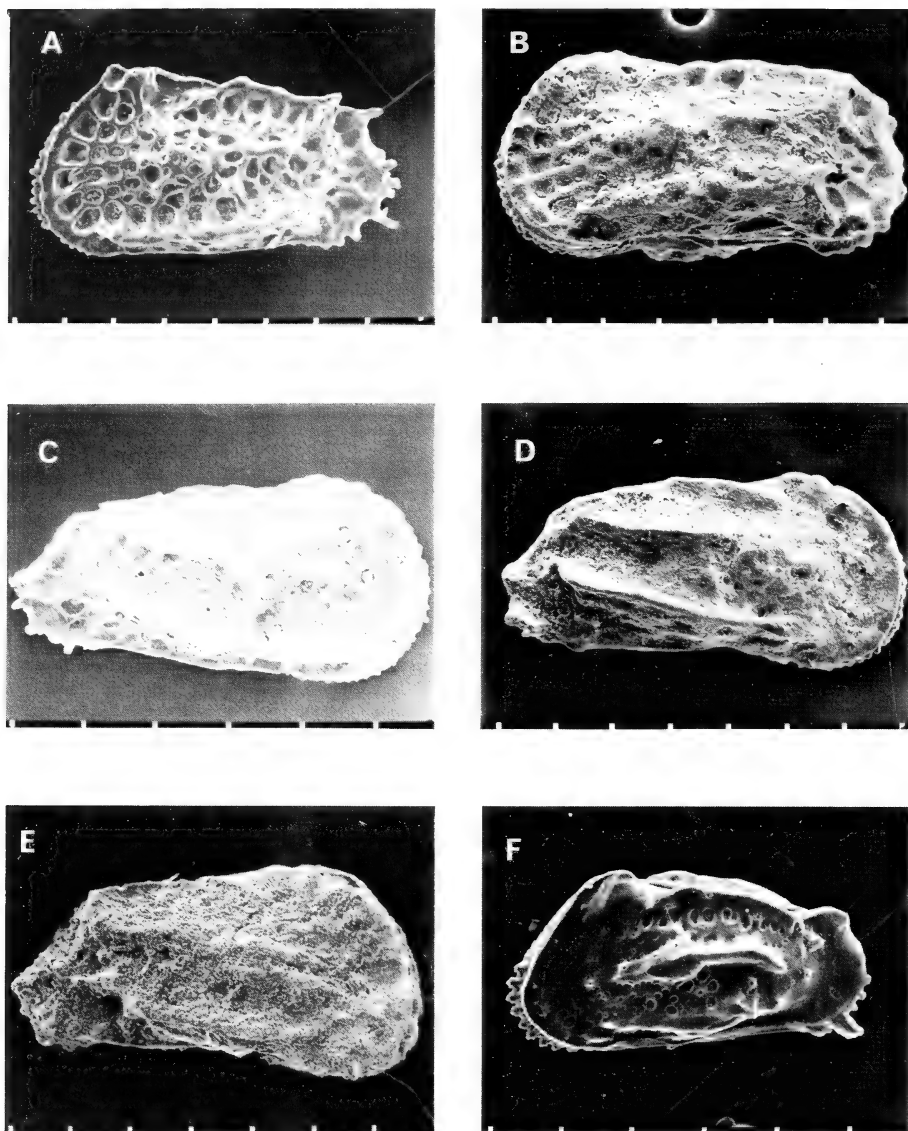


Fig. 51. A. *Hermanites kennedyi* Dingle, 1980, SAM-K5637, BH9 82.03 m, LV, Campanian II. B. *Hermanites kennedyi* Dingle, 1980, SAM-K5767, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian. C. *Hermanites? arcus* sp. nov., holotype, SAM-K5768, locality 20-1/3, Mfolozi River, RV, Maastrichtian I. D. *Hermanites? cf. H? arcus* sp. nov., SAM-K5769, Igoda Formation, Igoda estuary, RV, late Campanian/early Maastrichtian. E. *Hermanites? cf. H? arcus* sp. nov., SAM-K5770, Lower Quarry Needs Camp, RV, late Campanian/early Maastrichtian. F. *Rayneria nealei* Dingle, 1980, SAM-K5653, BH9 106.0 m, LV, Campanian I.
Scale bars all 100 μ .

posteriorly. Dorsal outline partially hidden by curved, ponticulate dorsolateral ridge that runs from posterodorsal angle to just behind the eye spot. Median ridge is connected to dorsal ridge at their respective posterior ends, and runs diagonally across the valve surface to anterior of the SCT. There is a curved ventral ridge which parallels the median ridge and connects to the AM ridge. The latter extends to the prominent eye spot, behind which it forms a small ear. Valve surface is coarsely reticulate all over. Fossae are polygonal and irregularly shaped, often partially rounded.

No internal features seen, hence provisional generic placement.

Remarks

The surface features of *H? arcus* bear a striking resemblance to those of *H. kennedyi*. The two species differ in the nature and disposition of the median-lateral ridge: in *arcus* it is diagonal and reaches the dorsal margin, whereas in *kennedyi* it is vestigial and roughly parallel to the line of greatest length.

Dimensions (mm)

	length	height
K5768	0,56	0,29
Other material	>0,50	0,30

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *H? arcus* is a rare species that in Zululand is restricted to assemblage 7, suggesting that it was environmentally bound by deep-water (?>500, outer shelf/upper slope), oceanographically stable conditions (Fig. 50B, Table 4). The temporal and environmental range of this species may be greater than the Zululand populations suggest (see below).

Hermanites? cf. H?. arcus sp. nov.

Fig. 51D–E

Remarks

Two specimens showing great similarity to *H?. arcus* were recovered from Igoda (SAM–K5769) and Needs Camp (SAM–K5770). Shell abrasion and secondary calcite crystallization prevent a detailed comparison of surface features, but the only noticeable difference with the Zululand specimens is the slightly weaker upward curvature of the ventrolateral ridge, and a more pronounced VM concavity immediately behind the SCT.

Dimensions (mm)

	length	height
K5769	0,70	0,34
K5770	0,68	0,35

Age, distribution, palaeoecology

If these specimens are conspecific with *H?. arcus* then they probably extend the known range of this species from late Campanian/early Maastrichtian (Igoda and Needs Camp) to Maastrichtian II (Zululand). They also indicate that it was capable of surviving in very shallow (20 m) moderate to high-energy environments (Needs Camp), although even in the slightly deeper (100–200 m) water of the Igoda Formation it occurs only in trace numbers.

Genus *Rayneria* Neale, 1975

Rayneria nealei Dingle, 1980

Fig. 51F

Rayneria nealei Dingle, 1980: 55–57, figs 28E–F, 29A–F, 30G.

Remarks

Only two specimens of this species have been recovered from strata younger than Santonian (Richards Bay RB–9 borehole) where it is at the top of its local range.

Age, distribution, palaeoecology

Santonian II to Campanian I. *R. nealei* occurs in ostracod assemblages 1–3 and 4a in which it is equitably, though sparsely distributed. In this respect its disappearance just above the base of Campanian I may be a useful biostratigraphic marker horizon in south-east Africa since it does not appear to be environmentally bound, except that all its occurrences seem to be in water no deeper than about 100 m.

Genus *Cythereis* Jones, 1849

This genus is represented by two species in the Campanian–Maastrichtian of south-east Africa: *C. transkeiensis* and *C. klinger*i. Both range from Santonian to Campanian/Maastrichtian, but whereas *C. transkeiensis* is known from Igoda, Umzamba, and the base of the Richards Bay BH–9 borehole, *C. klinger*i appears to be restricted to the northern area: BH–9 borehole and Mfolozi and Nibela outcrops in Zululand. In their respective geographical areas, each species is an important member of the cytheracean faunas, *C. klinger*i especially so.

*Cythereis klinger*i Dingle, 1980

Fig. 52A

*Cythereis klinger*i Dingle, 1980: 34–38, figs 18B–F, 19 A–F.

Remarks

The relatively wide range of intraspecific morphological variation noted by Dingle (1980) in the Santonian–Campanian I rocks of the Richards Bay BH–9 borehole also occurs in the younger outcrops in Zululand, although no environmentally related trends can be identified.

Age, distribution, palaeoecology

Santonian II to Maastrichtian II. *C. klinger* appears to be restricted to the northern area: Richards Bay BH-9 borehole and Mfolozi and Nibela outcrops, Zululand. Along with *Brachycythere longicaudata*, it is the most environmentally tolerant of the cytheracean taxa, occurring in all the ostracod assemblages so far identified (Table 4). However, it is most abundant in assemblages 3 and 6, particularly the former, where in the upper Santonian III of the Richards Bay BH-9 borehole it locally constitutes over 30 per cent of the total ostracod population. Within the Campanian-Maastrichtian strata it is most abundant in Campanian III (assemblage 6) where it locally constitutes >20 per cent cytheracean element (Fig. 50D-E, Table 4). From our other evidence, the two sedimentary environments represented by assemblages 3 and 6 do not appear to have much in common (shallow, <100 m, and deep ?>500 m, respectively) and the reason for the observed distribution is not known.

Cythereis transkeiensis Dingle, 1969

Fig. 52B-C

? *Cythereis ornatissima* Reuss, 1846, var. *reticulata* Jones & Hinde, 1890, Chapman, 1904: 234.
Cythereis transkeiensis Dingle, 1969: 377-378, fig. 18; 1980: 34, fig. 18A.

Remarks

This species has been found in Campanian-Maastrichtian strata only at Igoda (7% of total fauna) and Umzamba (one fragment). The Igoda population shows some small morphological differences to topotypic material and to the Santonian II specimens in the Richards Bay BH-9 borehole: its median and ventrolateral longitudinal ridges have somewhat sharper crests, the post-anterior cardinal angle depression on the DM is less pronounced, and the median depression post-adjacent to SCT is not well developed. In addition, the Igoda valves are somewhat more heavily calcified, but none of these differences is as great as the variations found within individual populations of *C. transkeiensis*.

Age, distribution, palaeoecology

?Santonian II to Campanian I (Umzamba), Santonian II (Richards Bay BH-9 borehole), late Campanian/early Maastrichtian (Igoda). *C. transkeiensis* appears to be restricted to Igoda, Umzamba and Richards Bay, with the latter locality marking the northern limit of its range. Within the Santonian, this species is associated with shallow, relatively high-energy sedimentary environments, but its presence at Igoda indicates that it also inhabited low to moderate-energy, moderate-depth (?100 m) sedimentary environments, suggesting that, like its northern counterpart *C. klinger*, *C. transkeiensis* was environmentally tolerant.

Genus *Gibberleberis* Dingle, 1969

Gibberleberis is one of the minor genera in the south-east African Upper Cretaceous, and has been recorded at only three horizons above the Santonian-

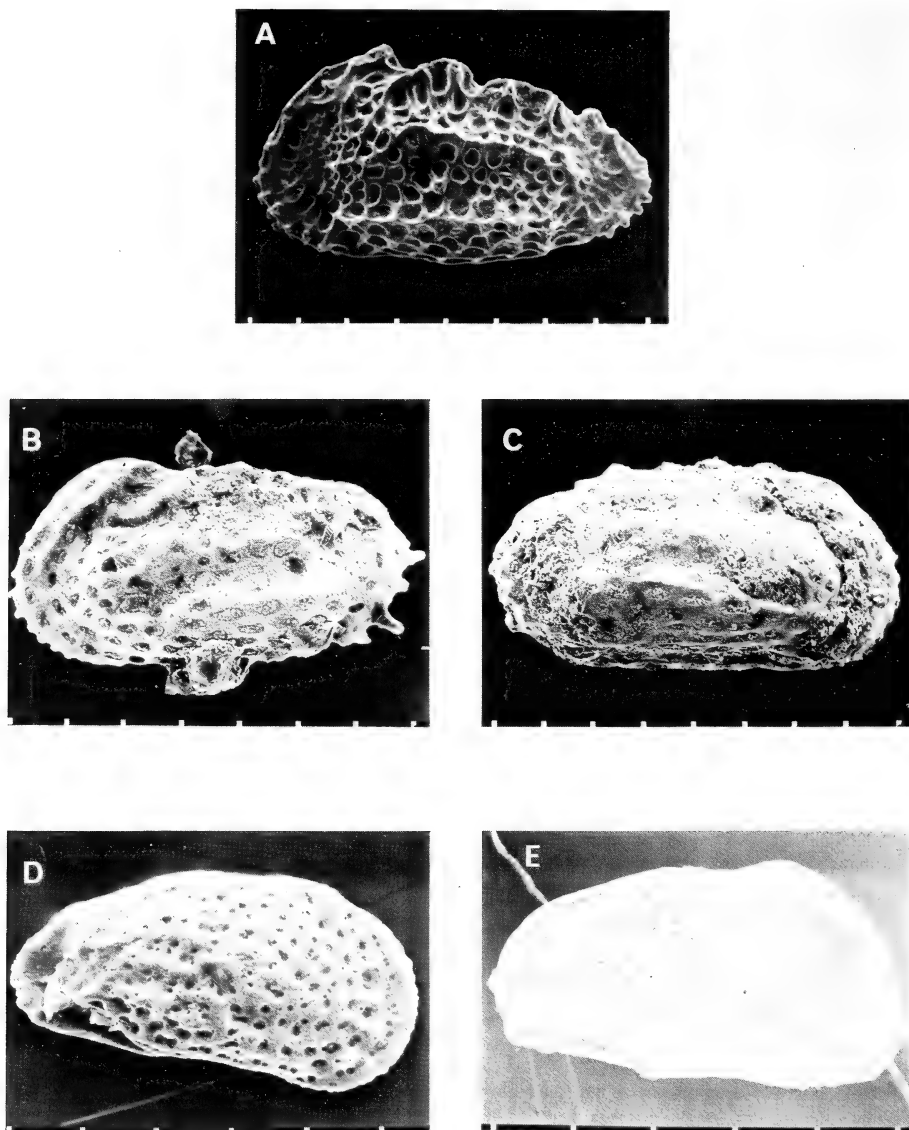


Fig. 52. A. *Cythereis klingerii* Dingle, 1980, SAM-K5617, BH9 82,03 m, LV, Campanian II. B-C. *Cythereis transkeiensis* Dingle, 1969, Igoda Formation Igoda estuary, late Campanian/early Maastrichtian. B. SAM-K5771, LV. C. SAM-K5772, RV. D. *Gibberleberis elongata* Dingle, 1980, SAM-K5773, BH9 88,76 m, RV, Campanian II. E. *Gibberleberis* sp. A, SAM-K5774, locality 110-14, Nibela Peninsula, RV, Campanian II.
Scale bars all 100 μ .

Campanian boundary, where it is represented by two species, *G. elongata* and *G. sp. A* (Fig. 50F–G). Although never abundant, *Gibberleberis* consistently occurs in the Santonian strata at Umzamba and in the Richards Bay BH–9 borehole (Dingle 1969, 1980), and appears to be at the upper limit of its range in the lower Campanian.

Gibberleberis elongata Dingle, 1980

Figs 52D, 53A

Gibberleberis elongata Dingle 1980: 57–59, figs 30E–F, 31A.

Remarks

A rare species first recorded from the Richards Bay BH–9 borehole and since located at one horizon (at locality 110, Nibela Peninsula) at outcrop.

Age, distribution, palaeoecology

Santonian III to Campanian II (Richards Bay BH–9 borehole, Nibela Peninsula, Zululand). *G. elongata* occurs in trace numbers in ostracod assemblages 2, 2–3 transition, 5a and 4b (Fig. 50F). It is not possible to determine a preference because of the small numbers of specimens found at each horizon, although the species seems to be restricted to water shallower than 300 m.

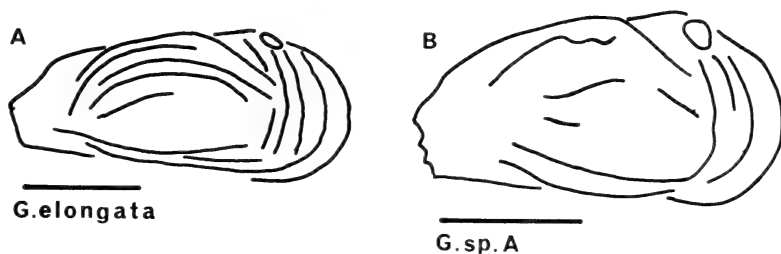


Fig. 53. Sketches of *Gibberleberis* species showing main rib patterns. A. *G. elongata* Dingle, 1980, SAM-K5660, BH9 124,0 m, RV, Santonian III. B. *G. sp. A*, SAM-K5774, locality 110–14, Nibela Peninsula, RV, Campanian II. Scale bars 200 μ .

Gibberleberis sp. A

Figs 52E, 53B

Remarks

One carapace of this species was found at locality 110 on the Nibela Peninsula. It resembles *G. africanus* Dingle, 1969, but differs in lacking a rib along the dorsal edge of the dorsolateral hump, in having a slightly different disposition of lateral ribs, in having a less coarsely reticulate surface ornamentation, and in lacking a well-defined posteroventral caudal process.

Dimensions (mm)

	length	height
K5774	0,50	0,28

Age, distribution, palaeoecology

Uppermost Campanian II (Nibela Peninsula, Zululand). It occurs in ostracod assemblage 4b, indicating that it was deposited in quiet, moderate-water depths (?200 m inner-mid shelf). This is the youngest record of the genus *Gibberleberis* so far.

Genus *Australileberis* Dingle, 1976

Records of this genus have previously been confined to the Eocene: JC-1 borehole off Natal; and outcrops on the Agulhas Bank (Dingle 1976).

Australileberis stangerensis sp. nov.

Fig. 54A-B

Derivation of name

Locality of JC-1 borehole, east of Stanger, Natal.

Holotype

SAM-K5775, RV, JC-1 borehole, 1 676 m, Maastrichtian.

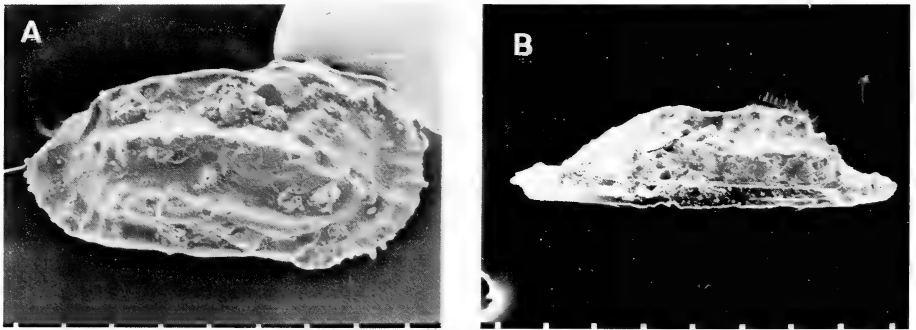


Fig. 54. *Australileberis stangerensis* sp. nov., SAM-K5775, JC-1 1676 m, Maastrichtian. A. Lateral view RV. B. Dorsal view RV.

Scale bars 100 μ .

Diagnosis

Species with thick AM rim, and sharp median longitudinal ridge.

Description

External features. In lateral view elongate, broadly rounded, weakly spinose AM, acuminate PM. Anterior area strongly depressed. DM and VM straight, converging posteriorly. Surface ornamented with three prominent longitudinal

ridges. Dorsal ridge is shortest and is medianly deflected behind large eye spot. Median ridge has a sharp crest and continues across the SCT as a narrow feature to a prominent pustule. Ventral ridge is also sharp crested, deflected medianly at its anterior end. There is a thick AM rim carrying small pustules, which passes, via a small flared anteroventral flange, to a narrow VM ridge. Intercoastal areas smooth, except for numerous perforate pustules.

Internal features. Hinge amphidont, all elements appear smooth, but may be slightly worn. MA wide with at least twenty-five long, thin anterior MPC, the anterodorsal ones of which curve upwards. Posterior MPC and MS not seen.

Remarks

A. stangerensis is very close, and presumably ancestral to *A. hieroglyphica*. The two species can be distinguished by the presence of a thick AM rim in *A. stangerensis*, which contrasts with the unrimmed compressed anterior area of *A. hieroglyphica*. Their surface ornamentation is similar, although the new species is closer to the Agulhas Bank populations of *A. hieroglyphica* than it is to the typically more heavily calcified varieties in JC-1 borehole. The holotype of *A. stangerensis* is significantly smaller than typical examples of the Tertiary species.

Dimensions (mm)

	length	height	width
K5775	0,80	0,40	0,19

Age, distribution, palaeoecology

Maastrichtian (level 1 676 m), JC-1 borehole. The horizon at which *A. stangerensis* occurs is within the mid-Maastrichtian charophytes-rich section of the borehole (Table 10). Other ostracod species are rare in this facies, which is thought to represent a level at which there were particularly large influxes of fluvial debris on to the Tugela delta top during local lower sea-level stands. This contrasts with the occurrence of *A. hieroglyphica* in the overlying Palaeogene. Here, this species is absent from the Palaeocene charophytes-bearing strata, and appears only in the normal marine Eocene sediments.

Genus *Trachyleberis* Brady, 1898

This genus is represented by three species in the Campanian–Maastrichtian strata of south-east Africa (Fig. 55): one long ranging (*T. zululandensis*), and two short ranging (*T. minima* and *T. schizospinosa*), and as far as is known the genus does not occur in rocks older than Campanian in this region. In the Campanian I to III it occurs sporadically, though locally constituting up to 10 per cent of the cytheracean population, but in the younger rocks it is consistently present, albeit in small numbers (2–10% of the cytheracean population) (Fig. 55). In the one sample that was available from the Maastrichtian III (on the Agulhas Bank), the genus (*T. schizospinosa*) constituted a remarkable 40 per cent of the cytheracean population (33% of the total ostracod population).

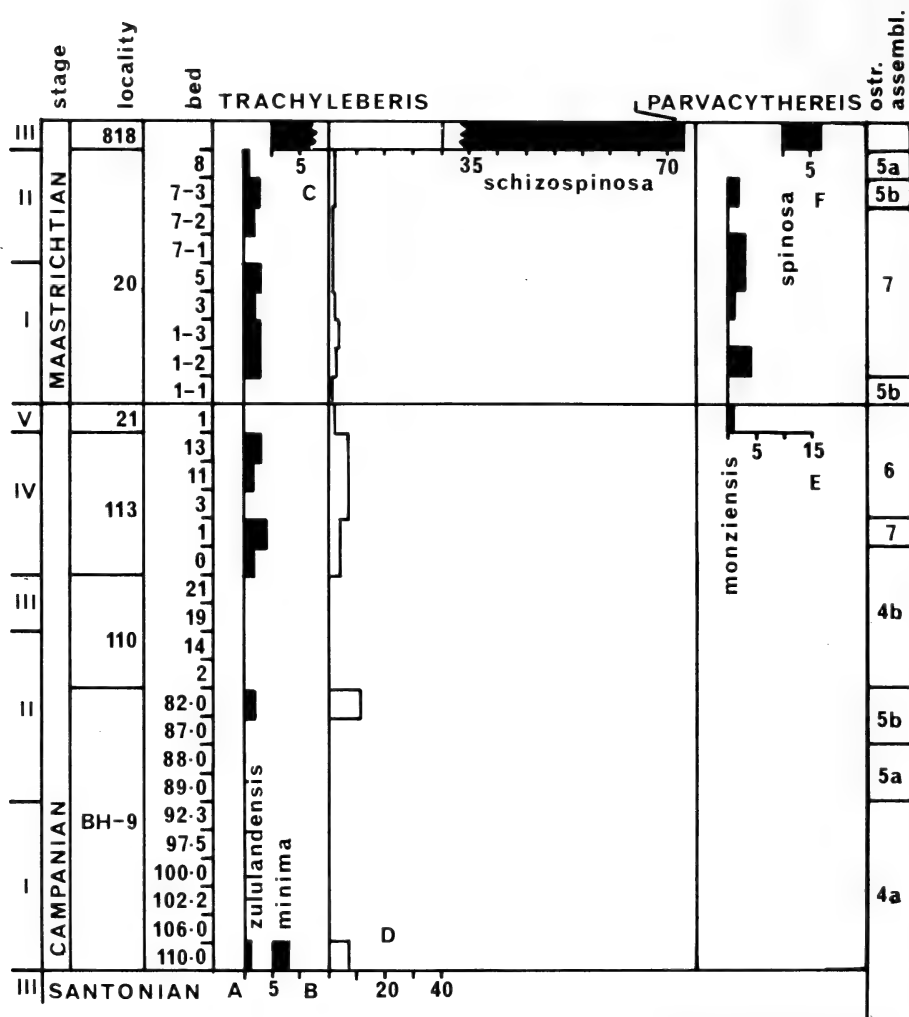


Fig. 55. Distribution of *Trachyleberis* and *Parvacythereis* in Campanian–Maastrichtian strata of Zululand and Agulhas Bank. A. Total number of valves of *Trachyleberis zululandensis*. B. Total number of valves of *Trachyleberis minima*. C. Total number of valves of *Trachyleberis schizospinosa*. D. *Trachyleberis* as percentage of Cytheracea. E. Total number of valves of *Parvacythereis monziensis*. F. Total number of valves of *Parvacythereis spinosa*.

Trachyleberis zululandensis Dingle, 1980

Figs 56A, 57B, D

Trachyleberis zululandensis Dingle, 1980: 52–54, fig. 28A–C.

Remarks

In his original description, Dingle (1980) recorded the species from two horizons in the Richards Bay BH-9 borehole. Considerably more material has now been obtained from outcrops in Zululand and one point of uncertainty with

regard to a possible assignment to the genus *Matronella* can be cleared up. The MS of the species, seen for the first time, definitely preclude such an assignment as they show a hooked anterior and four complete posterior adductors (Fig. 57D). The second adductor is, however, medianly constricted. There is no similarity to the 'splintered' (*élatées*) arrangement described by Damotte (1974) in her diagnosis of *Matronella*. A further point that should be emphasized is the slight difference in shape between LV and RV. The former are more rectangular than the somewhat triangular-shaped RV (compare Figs 56A and 57B).

Age, distribution, palaeoecology

Campanian I to Maastrichtian II (Richards Bay BH-9 borehole, Mfolozi and Nibela outcrops, Zululand). *T. zululandensis* is an environmentally tolerant species, having been found in ostracod assemblages 4a, 4b, 5a, 5b, 6-7 (Fig. 55A, Table 4), but, as suspected by Dingle (1980), it has a distinct preference for deep-water environments, particularly that represented by assemblage 6: deep water (>500 m outer shelf/upper slope), with oceanographically unstable conditions.

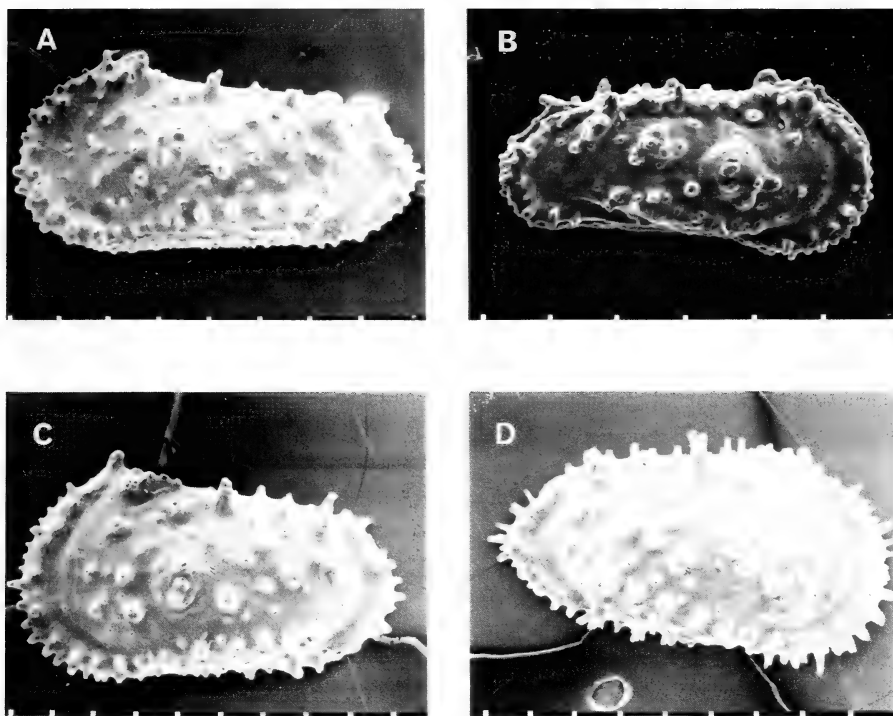


Fig. 56. *Trachyleberis*. A. *T. zululandensis* Dingle, 1980, SAM-K5776, locality 113-1, Nibela Peninsula, LV, Campanian IV. B. *T. minima* Dingle, 1980, SAM-K5654, BH9 110.0 m, RV, Campanian I. C-D. *T. schizospinosa* Dingle, 1971, TBD 818 Alphonse Formation, Agulhas Bank, Maastrichtian III. C. SAM-K5777, LV. D. SAM-K5778, RV.

Scale bars all 100 μ .

Trachyleberis minima Dingle, 1980

Fig. 56B

Trachyleberis minima Dingle, 1980: 54, fig. 28D.**Remarks**

No further specimens of this rare species have been recorded since the original description for the Richards Bay BH-9 borehole.

Age, distribution, palaeoecology

Lowermost Campanian I (Richards Bay BH-9 borehole). The only record has been from ostracod assemblage 5a, which is reckoned to represent quiet moderate depths (?200–300 m mid-outer shelf).

Trachyleberis schizospinosa Dingle, 1971

Figs 56C–D, 57A

Trachyleberis schizospinosa Dingle 1971: 406–408, figs. 9–10, pl. 1a.**Remarks**

Although we have no additional data on this species, SEM photographs are reproduced herein to supplement the original descriptions. In comparison with

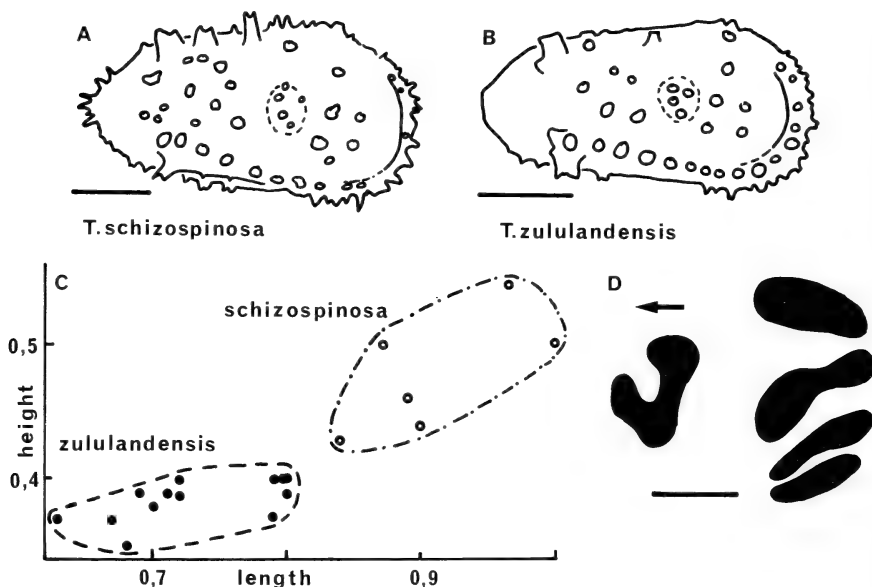


Fig. 57. *Trachyleberis*. A–B. Sketches showing valve outline and arrangement of spines and nodes. A. *T. schizospinosa* Dingle, 1971, SAM-K5778, TBD 818 Alaphard Formation, Agulhas Bank, RV, Maastrichtian III. B. *T. zululandensis* Dingle, 1980, SAM-K5779, locality 20–5, Mfolozi River, RV, Maastrichtian I. C. Length v. height scattergram of adult *T. zululandensis* (dots) and *T. schizospinosa* (circles). D. *T. zululandensis* Dingle, 1980, SAM-K5780, locality 20–5, Mfolozi River, MS RV, Maastrichtian I.

Scale bars: A–B = 200 μ , D = 30 μ .

T. zululandensis, *T. schizospinosa* is seen to be plumper, and consistently possesses a ring or cluster of small spines midway between, and slightly posterior to, the large posterodorsal and posteroventral spinose processes (Fig. 57A, B). It is also a considerably larger species (Fig. 57C).

Age, distribution, palaeoecology

Maastrichtian III (sample 818 Agulhas Bank) which is thought to represent an unusual setting: a quiet, shallow-water environment on the outer edge of the continental shelf or on the uppermost continental slope. In this fauna, *T. schizospinosa* constitutes 33 per cent of the total ostracod population.

Genus *Parvacyptheris* Gründel, 1973

Gründel (1973) quoted a range of ?Cenomanian to upper Tertiary for this genus, and suggested that it evolved from *Cornicytheris*. To our knowledge, the two species found in the Campanian–Maastrichtian of south-east Africa are the first record of *Parvacyptheris* from the southern hemisphere, although two forms described by Bate (*in* Bate & Bayliss 1969) and Ducasse & Grekoff (1976) from the east Africa area may belong to it.

In south-east Africa, the genus constitutes a minor (up to 7%) but characteristic element in the Maastrichtian cytheracean populations.

Parvacyptheris monziensis sp. nov.

Figs 58A–E, 60A

Derivation of name

Locality of type, vicinity of Monzi village.

Holotype

SAM–K5781, RV, locality 20–7/1, Mfolozi River, Maastrichtian II

Paratypes

SAM–K5782, carapace, locality 20–7/1, Mfolozi River, Maastrichtian II

SAM–K5783, LV, locality 20–5, Mfolozi River, Maastrichtian I

SAM–K5784, RV, locality 20–3, Mfolozi River, Maastrichtian I

Diagnosis

Species with recurved ventrolateral rib and a round SCT.

Description

External features. In lateral view AM broadly rounded, PM bluntly triangular. DM and VM almost straight, converging posteriorly. Strong, narrow AM rim which commences over prominent eye spot, and is continuous with a VM rib that recurves at a posteroventral process and runs forward to below the prominent, rounded SCT. The SCT possesses a small, curved anteroventrally

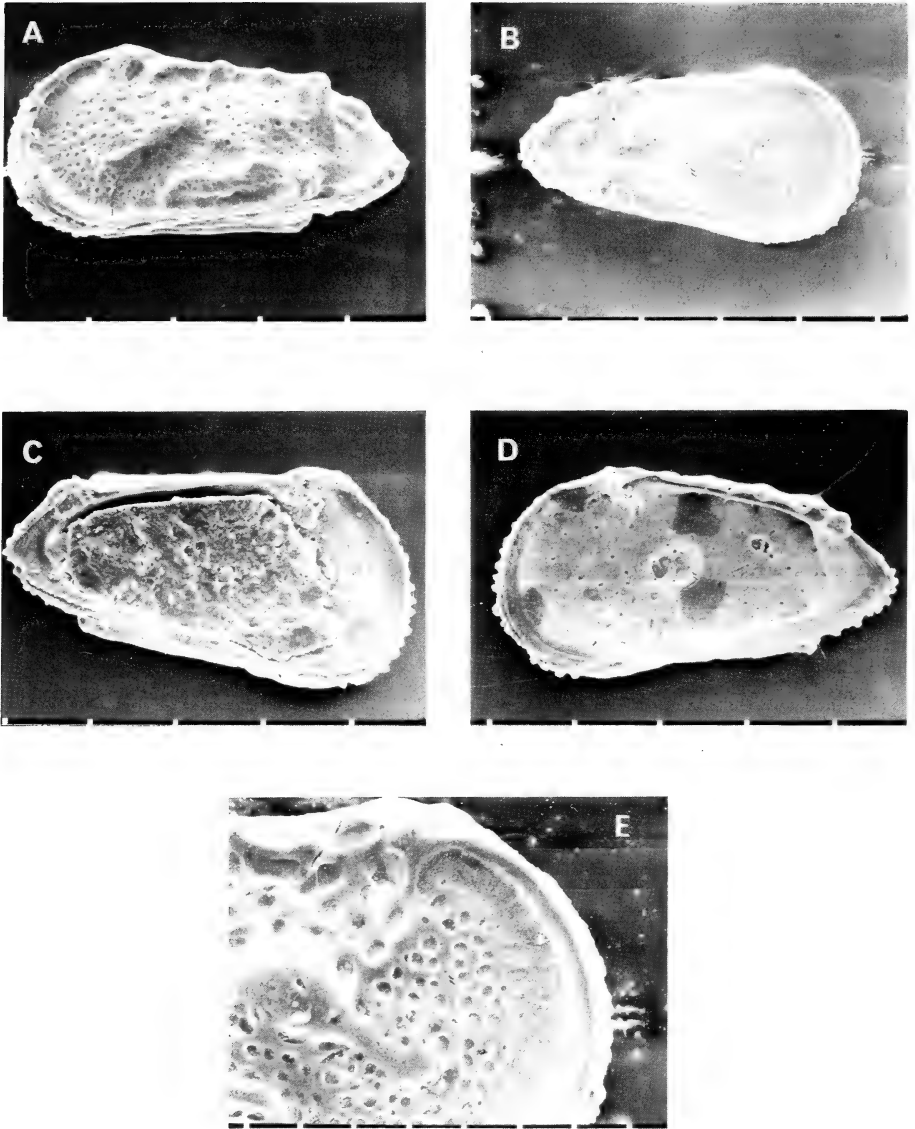


Fig. 58. *Parvacyntheris monziensis* sp. nov. A. SAM-K5782, locality 20-7/1, Mfolozi River, LV, Maastrichtian II. B. Holotype, SAM-K5781, locality 20-7/1, Mfolozi River, RV, Maastrichtian II. C. SAM-K5783, locality 20-5, Mfolozi River, internal LV, Maastrichtian I. D. SAM-K5784, locality 20-3, Mfolozi River, internal RV, Maastrichtian I. E. Holotype, SAM-K5781, locality 20-7/1, Mfolozi River, RV, Maastrichtian II.
Scale bars: E = 30 μ , others = 100 μ .

directed projection. There is a small rounded isolated median process post-adjacent to the SCT. Dorsolateral rib is weakly developed, is not connected to the eye spot, and ends in at an angular posterodorsal node. Valve surface is coarsely punctate with smaller fossae in the anterior area. Fossae are generally rounded and well separated, but immediately adjacent to the marginal ribs they are larger and quadrate.

Internal features. MA moderately wide, but no good views of MPC available. Hinge is apparently holamphidont. MS consist of a hooked anterior scar and four adductors. The second scar is the largest and is a 'dog's bone' shape, whilst the first scar has a dorsal extension.

Remarks

P. monziensis differs from the genotype *P. subparva* (Pokorny 1967) (as redescribed by Gründel 1973), by lacking a distinctly concave VM and in possessing a recurved ventral ridge. It is very close to *P. spinosa* from the Maastrichtian III of the Agulhas Bank, but differs in having a less pronounced triangular valve outline (particularly in the RV) and in having a rounded SCT, rather than the ovate feature of *P. spinosa*. Their close relationship suggests that *P. spinosa* evolved from *P. monziensis* during the middle-upper Maastrichtian.

P. monziensis also bears a resemblance to a lower Eocene form referred to *Hazelina* sp. 4 from core number 9 at DSDP site 246 off east Africa (Ducasse & Grekoff 1976), and to *Curfsina turonica* Bate, 1969 (in Bate & Bayliss 1969) from the Turonian of Tanzania. It is possible that both the latter species should be assigned to the genus *Parvacythereis*.

P. monziensis has been selected as a subzonal species for part of the *Dutoitella dutoiti* Zone proposed herein.

Dimensions (mm)

	length	height
K5781	0,43	0,22
K5782	0,45	0,21
K5783	0,47	0,25
K5784	0,46	0,23
Other material	0,44	0,24
Other material	0,42	0,22
Other material	0,44	0,22

Age, distribution, palaeoecology

Campanian V to Maastrichtian II (Monzi and Mfолоzi areas, Zululand). *P. monziensis* has been recorded from assemblages 5b, 6, and 7 (Fig. 55E, Table 4), but its patchy distribution in the first two indicates that although it tolerated conditions that ranged shoreward to mid shelf (?300–500 m), it preferred deep water (> 500 m outer shelf/upper slope) with oceanographically stable environments.

Parvacypthereis spinosa (Dingle, 1971)

Figs 59A–C, 60B

Phacorhabdotus spinosa Dingle, 1971: 408–410, fig. 11.*Remarks*

As pointed out by Dingle (1971), although the lateral outline is typical of the genus *Phacorhabdotus*, to which it was originally assigned, its ornamentation differs from other species within the genus. Its translation to *Parvacypthereis* removes this anomaly.

P. spinosa is very close to *P. monziensis* sp. nov., but the two can be differentiated in the distinctly more triangular lateral outline of the former (especially in RV), on the shape of the SCT which is rounded in *P. monziensis* and anteriorly elongated in *P. spinosa*, and on the somewhat more prominent dorsal ridge of *P. spinosa*. Although not clearly visible, under high magnification the MS of *P. spinosa* are very similar to those of *P. monziensis* with the second adductor being the largest (Fig. 60A–B).

Age, distribution, palaeoecology

Maastrichtian III (sample 818 Agulhas Bank). The ostracod assemblage of sample 818 is thought to represent an unusual setting: a quiet, shallow-water environment on the outer edge of the continental shelf or on the uppermost continental slope.

Genus *Phacorhabdotus* Howe & Laurencich, 1958*Phacorhabdotus? anomala* Dingle, 1971

Fig. 59D–E

Phacorhabdotus? anomala Dingle, 1971: 410–411, fig. 12.*Remarks*

An SEM view of the holotype (Agulhas Bank) is included herein to supplement the original description. Although the specimen from JC–1 borehole is crushed, the essential morphological elements are visible and allow a confident assignment. Bate (*in* Bate & Bayliss 1969, pl. 8 figs 8–9, 12) has recorded a very similar species from the Maastrichtian of Tanzania: *Phacorhabdotus* sp.

Age, distribution, palaeoecology

Maastrichtian III (sample 818 Agulhas Bank), Maastrichtian (level 1 625 m) JC–1 borehole. The ostracod assemblage of sample 818 is thought to represent an unusual setting: a quiet, shallow-water environment on the outer edge of the continental shelf or on the uppermost continental slope, whilst level 1 625 m in the upper part of the JC–1 Maastrichtian was probably deposited during a period of relatively deep-water (100–200 m) conditions on the Tugela delta top.

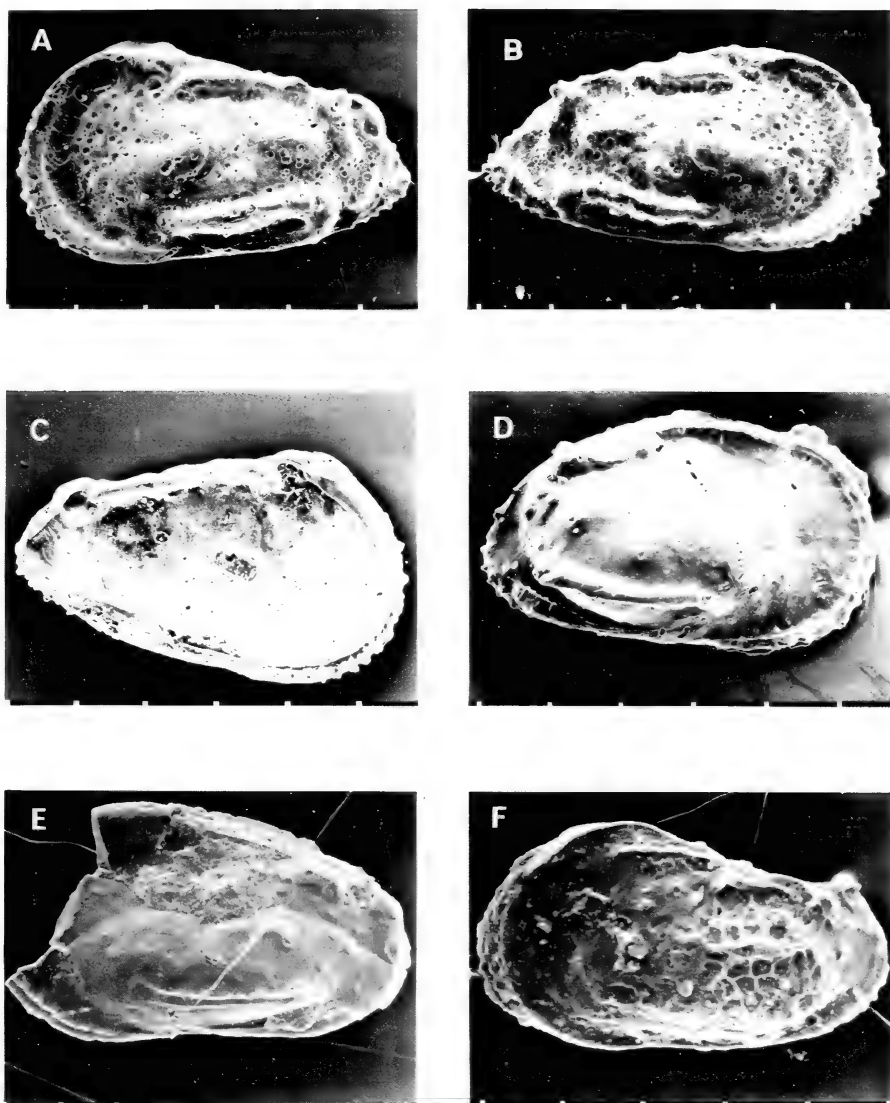


Fig. 59. A-C. *Parvacyptheris spinosa* (Dingle, 1971), TBD 818 Alaphard Formation, Agulhas Bank, Maastrichtian III. A. SAM-K5785, LV. B. SAM-K5786, RV. C. SAM-K5787, internal LV. D-F. *Phacorhabdotus?* D. *P? anomala* Dingle, 1971, holotype, MG-4-1-18, TBD 818 Alaphard Formation, Agulhas Bank, RV, Maastrichtian III. E. *P? anomala* Dingle, 1971, SAM-K5788, JC-1 1625 m, LV, Maastrichtian. F. *P? sp. A*, SAM-K5789, JC-1 1756 m, LV, Maastrichtian. Scale bars all 100 μ .

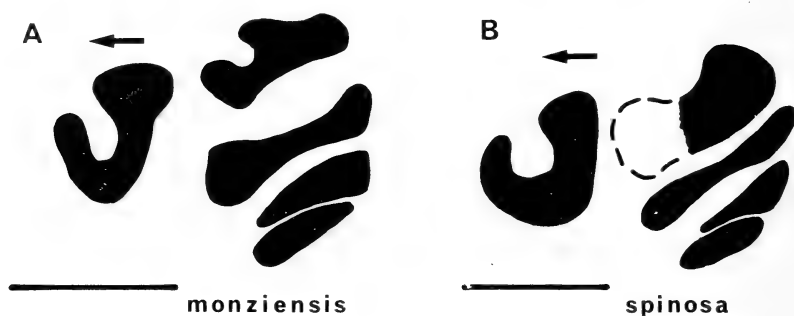


Fig. 60. Muscle scars of *Parvacypthereis*. A. *P. monziensis* sp. nov., SAM-K5784, locality 20-3, Mfolozi River, RV, Maastrichtian I. B. *P. spinosa* (Dingle, 1971), TBD 818 Alphard Formation, Agulhas Bank, RV, Maastrichtian III. Scale bars 30 μ .

Phacorhabdodus? sp. A

Fig. 59F

Remarks

One valve with the characteristic external morphology of the genus was recovered from the JC-1 borehole. No internal views were available so generic assignment is provisional. Preservation is not good, but well-developed intercostal reticulation is present, as well as occasional conjunctive perforate pustules.

Age, distribution, palaeoecology

Maastrichtian (level 1 756 m) JC-1 borehole. *Phacorhabdodus?* sp. A occurs, together with *Bythocypris?* sp. and *Cytherella* sp., at levels that are thought to have been intermediate between the deeper (?200 m) and ?shallower (with large fresh-water influxes) water environments (Table 10) on the Tugela delta top.

Genus *Curfsina* Deroo, 1966

Within the Indian Ocean area this genus has previously been reported from the Turonian of Tanzania (Bate & Bayliss 1969) and the Campanian of Western Australia (Bate 1972). In south-east Africa it has been found at one locality only, where it constitutes 18 per cent of the cytheracean population (4% total ostracods).

Curfsina monziensis sp. nov.

Fig. 61A-D

Derivation of name

Locality of type.

Holotype

SAM-K5790, LV, locality 21-1, Monzi, Campanian V

Paratypes

SAM-K5791, RV, locality 21-1, Monzi, Campanian V

SAM-K5792, RV, locality 21-1, Monzi, Campanian V

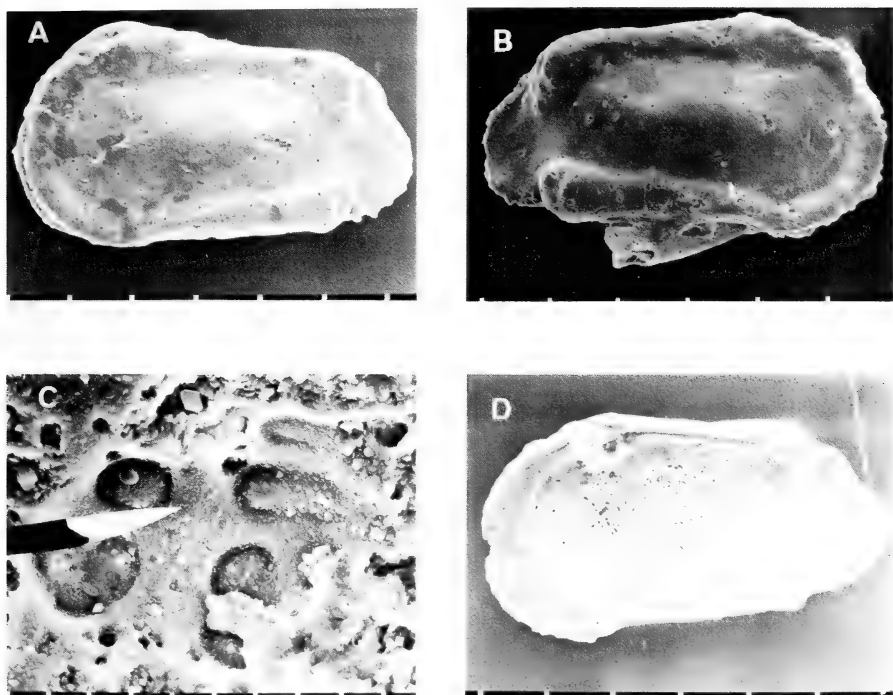


Fig. 61. *Curfsina monziensis* sp. nov., locality 21-1, Monzi, Campanian V. A. Holotype, SAM-K5790, LV. B. SAM-K5791, RV. C. SAM-K5792, MS RV. D. SAM-K5792, internal RV.

Scale bars: C = 10μ , others = 100μ .

Diagnosis

Smooth species with a stepped, peg-like ATE in RV hinge.

Description

External features. In lateral view, rectangular with rounded AM, slightly acuminate PM, and straight, slightly converging DM and VM. There is a broad, rounded AM rim, which is continuous with wide, rounded dorsal and ventral ribs that both end in posterior swellings. A median elevation, commencing over a SC swelling, projects and narrows posteriorly, where it curves towards the posterior end of the dorsal rib. These two elevations are separated by a narrow depression. Valve surfaces are completely smooth except for small punctae (about 5μ across). There is a large, but weak, eye spot in both valves: in RV it lies on the anterior cardinal angle, in LV below a smooth anterior cardinal swelling.

Internal features. Hinge holamphidont, but PTE is weakly subdivided and RV ATE is a stepped smooth peg. MS consist of a kidney-shaped anterior scar, with a rounded scar above it, and a vertical row of 4 adductors: the top two are oblong, the lower two rounded. MA generally narrow, no vestibule. MPC fine and straight, up to twenty anteriorly.

Remarks

C. monziensis is close to *C. levigata* Bate from the Campanian of Western Australia, but differs in not possessing a subdivided ATE, in having its median lateral rib separated from its dorsal rib, and in having continuous ventral and anterior ribs. The two species also have a slightly different MS pattern.

In his generic diagnosis, Deroo (1966: 139) states that the anterior MS is capped by a small oval scar. In *C. monziensis* this small scar is distinctly separate from the reniform anterior scar.

Dimensions (mm)

	length	height
K5790	0,62	0,36
K5791	0,59	0,31
K5792	0,60	0,33

Age, distribution, palaeoecology

Campanian V (locality 21, Monzi, Zululand). *C. monziensis* has been found only at locality 21, in a population that belongs to assemblage 6: deep water (?>500 m, upper continental slope) with unstable oceanographic conditions.

Genus *Cativella* Coryell & Fields, 1937

Cativella? dubia sp. nov.

Fig. 62A–B

Derivation of name

Latin *dubius* (uncertain): reference to uncertain taxonomic status.

Holotype

SAM-K5793, LV, locality 20–7/2, Mfolozi River, Maastrichtian II

Paratype

SAM-K5794, RV, locality 20–1/2, Mfolozi River, Maastrichtian I

Diagnosis

Species in lateral view having curved dorsal and ventral ridges that terminate in median deflections, intercostal areas are reticulate.

Description

External features. A small species, with, in lateral view, AM broadly rounded, PM strongly acuminate, spinose ventrally. VM almost straight, DM

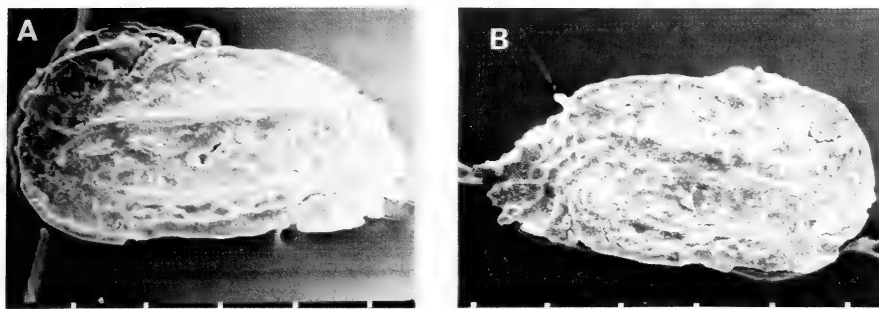


Fig. 62. *Cativella? dubia* sp. nov. A. Holotype, SAM-K5793, locality 20-7/2, Mfolozi River, LV, Maastrichtian II. B. SAM-K5794, locality 20-1/2, Mfolozi River, RV, Maastrichtian I. Scale bars 100 μ .

hidden by lateral ridge, but straight, strongly sloping posteriorly. Highest point of valve over anterior cardinal angle, greatest length below median line. Surface ornamentation dominated by ribs. There is a narrow AM rib that runs from the large eye spot, and is continuous with a VM rib that continues to the posterior end of the valve. DM is hidden behind a rib that curves medianly at both ends. A ventrolateral rib, curved medianly at both ends, runs parallel to a median rib which runs slightly diagonally across the central part of the valve. This median rib is hooked at its posterior end, and anterior of a point over the MS area is accompanied by a further, short, parallel rib. Intercostal areas are reticulate, with quadrate fossae and disjunctive and conjunctive pustules. Reticulation is coarser in the compressed anterior area, with small perforate pustules within fossae. LV and RV differ slightly in shape, there being a curved dorsal valve extension over the eye spot in LV.

Internal features. No internal features seen.

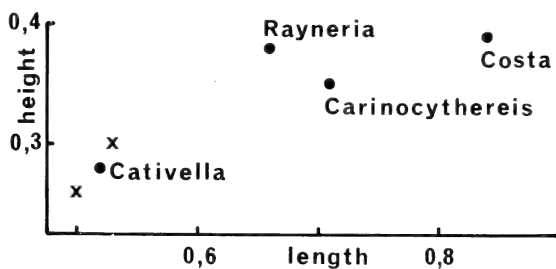


Fig. 63. Length v. height scattergram of holotypes of *Cativella*, *Rayneria*, *Carinocythereis* and *Costa* (dots) compared to specimens of *Cativella? dubia* (crosses) from Maastrichtian of Zululand.

Remarks

Generic assignment is uncertain because internal views are not available, and because the external features cannot be fitted unreservedly into any described genus. Four genera have various features in common with the new

species: *Costa*, *Rayneria*, *Carinocythereis* and *Cativella*. The first three, whilst possessing similar rib patterns, lack its posterior outline and are considerably larger (Fig. 63). *Cativella* is closest, but the genotype differs in possessing a slightly different rib pattern, although other species (e.g. *Cativella semitranslucens* (Crouch) quoted by Van Morkhoven 1963) are more similar. *Cativella* is considered a typical Tertiary taxon and most species that have been unequivocally allocated to it have been recorded from Central and South America. The only South Atlantic record is of *C. moriahensis* van den Bold, by Neufville (1979) from the Lower Eocene of eastern Brazil.

Dimensions (mm)

	length	height
K5793	0,53	0,30
K5794	0,50	0,26

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). *C? dubia* is environmentally bound to conditions represented by ostracod assemblage 7: deep water (?>500 m outer shelf/upper continental slope), oceanographically stable.

Genus *Paraplatycosta* Dingle, 1971
Paraplatycosta reticulata Dingle, 1971
 Fig. 64A-E

Paraplatycosta reticulata Dingle, 1971: 416, fig. 16, pl. 8C.

Remarks

No further specimens of this species have been recovered from the Upper Cretaceous of south-east Africa. SEM photographs of topotypes are included to supplement the original descriptions.

Age, distribution, palaeoecology

Maastrichtian III (sample 818 Agulhas Bank). The ostracod assemblage of sample 818 is thought to represent an unusual setting: a quiet, shallow-water environment in the outer edge of the continental shelf or on the uppermost slope.

Indeterminate taxa

Indet. sp. 1
 Fig. 65A

Remarks

Single battered valve of reticulate, trachylerid-like species. May belong to *Oertliella*.

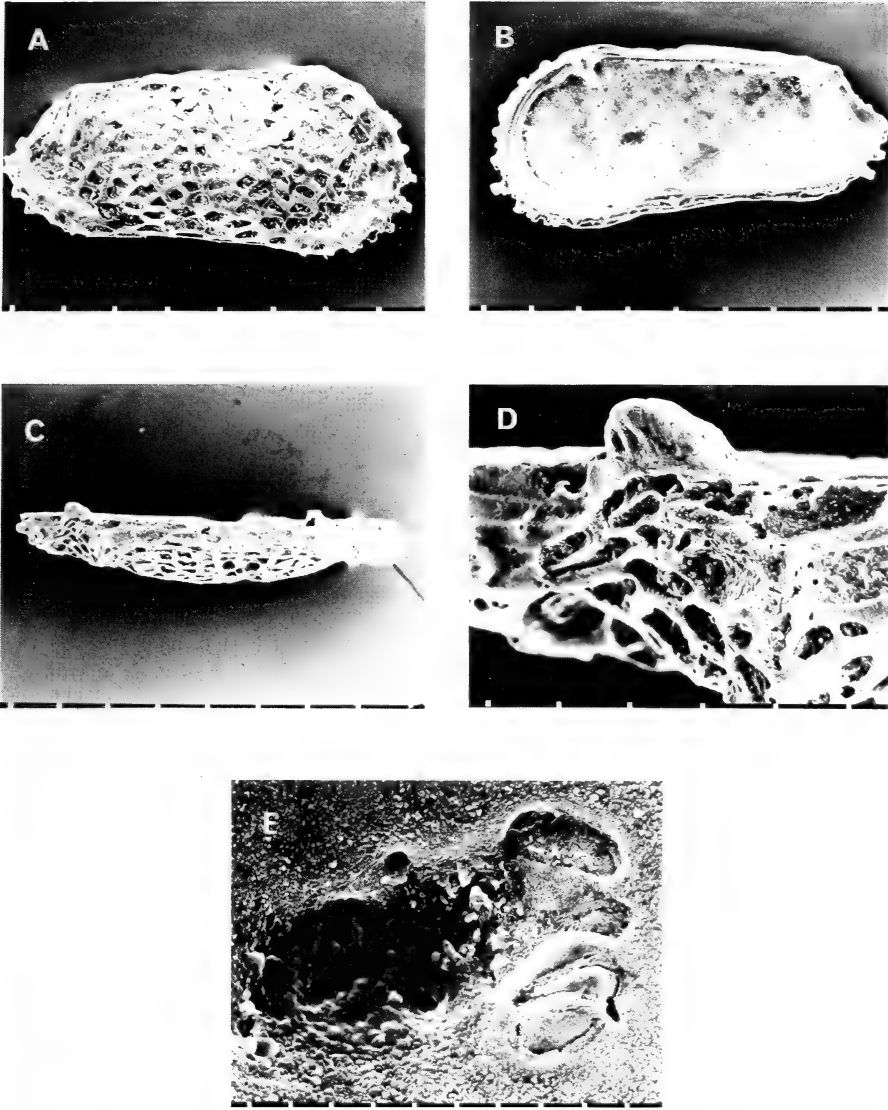


Fig. 64. *Paraplatycosta reticulata* Dingle, 1971, TBD 818 Alphard Formation, Agulhas Bank, Maastrichtian III. A. SAM-K5795, RV. B. SAM-K5796, internal RV. C. SAM-K5797, dorsal view RV, anterior to right. D. SAM-K5797, dorsal view PTE RV. E. SAM-K5796, MS RV.

Scale bars: D = 30μ , E = 10μ , others = 100μ .

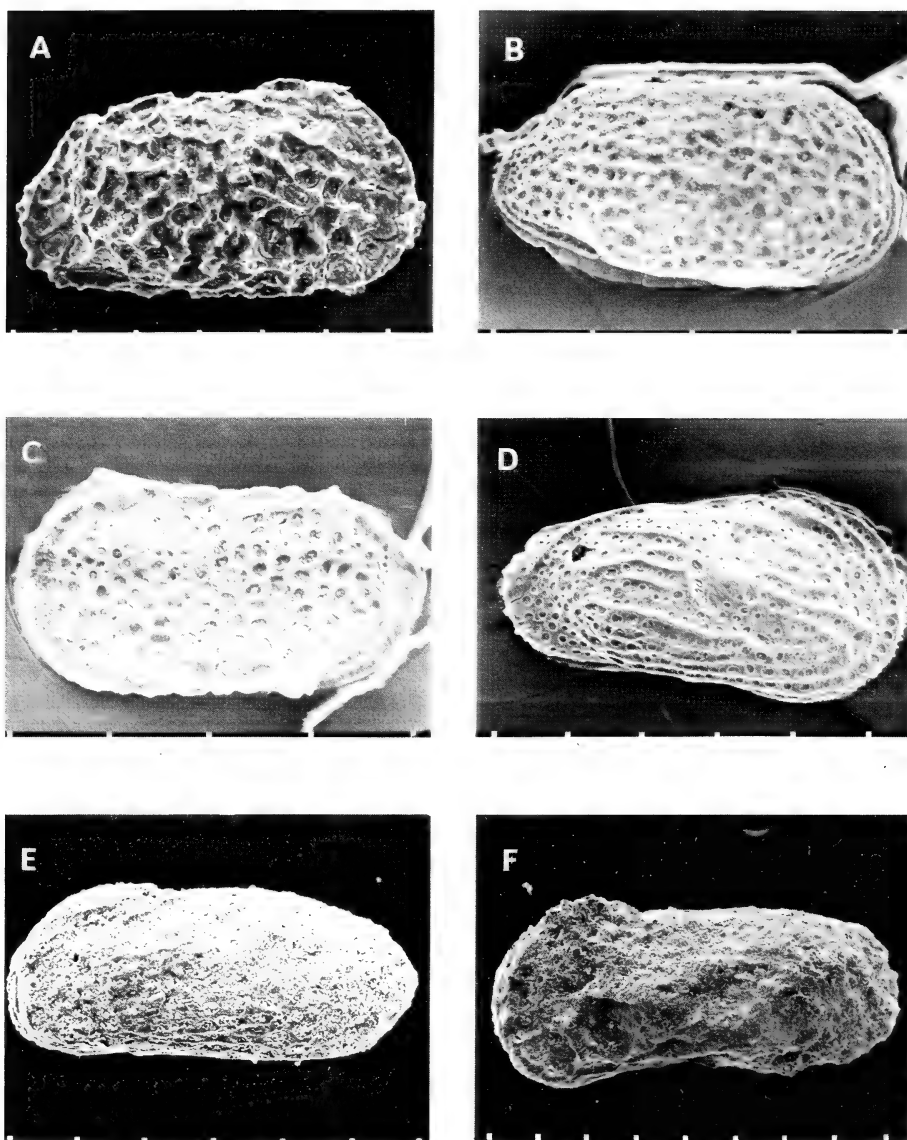


Fig. 65. Indeterminate species. A. Indet. sp. 1, SAM-K5798, locality 20-7/1, Mfolozi River, RV, Maastrichtian II. B. Indet. sp. 2, SAM-K5799, locality 20-1/2, Mfolozi River, RV, Maastrichtian I. C. Indet. sp. 3, SAM-K5800, locality 20-7/3, Mfolozi River, LV, Maastrichtian II. D. Indet. sp. 4, SAM-K5801, locality 20-7/3, Mfolozi River, RV, Maastrichtian II. E. Indet. sp. 5, SAM-K5802, Igoda Formation, Igoda estuary, LV, late Campanian/early Maastrichtian. F. Indet. sp. 6, SAM-K5803, Lower Quarry Needs Camp, LV, late Campanian/early Maastrichtian.

Scale bars all 100 μ .

Age, distribution, palaeoecology

Maastrichtian II (Mfolozi River, Zululand). Ostracod assemblage 7.

Indet. sp. 2

Fig. 65B

Remarks

Carapace, small, wholly reticulate species with a strong ventrolateral overhang. No eye spot or costation.

Age, distribution, palaeoecology

Maastrichtian I (Mfolozi River, Zululand). Ostracod assemblage 7.

Indet. sp. 3

Fig 65C

Remarks

Single valve of *Eucytherura*-like species with prominent eye spot. There is a small posterodorsal process, and a more prominent posteroventral process at the end of a blade-like and anteriorly-upturned ventrolateral ridge. Surface reticulate overall. No true caudal process.

Age, distribution, palaeoecology

Maastrichtian II (Mfolozi River, Zululand). Ostracod assemblage 5b.

Indet. sp. 4

Fig. 65D

Remarks

Two valves of a small, delicately ornamented species with fine, inclined longitudinal ribs in the central area of lateral view, and marginal, parallel ribs in anterior and ventral areas. Intercostal areas with scattered, small rounded fossae. There is a subdued SCT and a small eye spot. Grosdidier (1979) has illustrated a superficially similar specimen which he called *Dumontina*? GAD12 from the Turonian of Gabon. Our species is not a *Dumontina*, nor is it *Triginglymus* which is a further superficially similar specimen from lower Eocene from DSDP site 246 (Ducasse & Grekoff 1976).

Age, distribution, palaeoecology

Maastrichtian I to Maastrichtian II (Mfolozi River, Zululand). Ostracod assemblages 7 and 5a.

Indet. sp. 5

Fig. 65E

Remarks

Carapace of elongate-ovate, reticulate species with prominent ovate eye spot. Reminiscent of the more elongate varieties of *Haughtonileberis fissilis* from Umzamba, but poor preservation precludes detailed comparisons.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian Igoda Formation.

Indet. sp. 6

Fig. 65F

Remarks

Poorly preserved carapace of a *Hermanites*-like species. The only evidence of original ornamentation is coarse reticulation in the anteroventral area.

Age, distribution, palaeoecology

Late Campanian/early Maastrichtian, Lower Quarry Needs Camp.

Indet. sp. 7

Fig. 66A-B

Remarks

Carapace of an inflated spinose and pustulate blind species. The author suspects that it may be related to the genus quoted as *Acanthocythereis*? by Benson (1977).

Age, distribution, palaeoecology

Maastrichtian, borehole JC-1 (level 1 676 m). The only record of this species is from within the mid Maastrichtian section with abundant charophytes

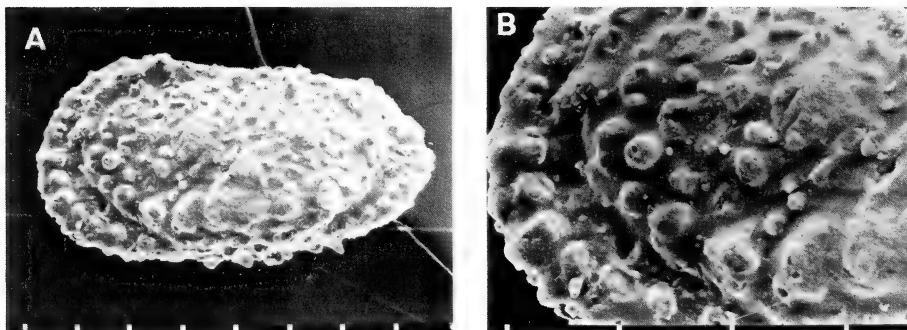


Fig. 66. Indeterminate species 7, SAM-K5804, JC-1 1676 m, Maastrichtian. A. Lateral view LV. B. Detail anterior area LV.
Scale bars 100 μ .

(same horizon as *Australileberis stangerensis*), where large influxes of fresh-water debris on to the Tugela delta top are suspected during a local low sea-level stand.

DISCUSSION

All the ostracods encountered were benthic types, and a total of 78 species belonging to 46 genera were identified in the Campanian–Maastrichtian strata of south-east Africa. Their spatial and temporal distributions are shown in Tables 1 and 2. It is convenient to commence a survey of the ostracod faunas by discussing the populations on a geographical basis before attempting a regional stratigraphic synthesis. In this connection, the composite succession from the various outcrops and the BH-9 borehole in Zululand is by far the most complete, and provides to a first approximation an unbroken section through the Campanian–Maastrichtian. The ostracod faunas from this area will, therefore, be used as a standard for comparison, and will allow correlation with the ammonite stratigraphy established by Kennedy & Klinger (1975 et seq.).

In his study of the Santonian–Campanian ostracods of the Richards Bay BH-9 borehole, Dingle (1980) used two principal techniques to discriminate significant faunal associations. The first highlighted the specific composition of the ostracod populations, with particular emphasis on dominant (>20%) and rare or marker types, coupled with population trends such as variations in species turnover and population similarity. The second technique demarcated fields of population similarity on a Cytheracea/Cytherellidae/Bairdiacea + Cypridacea triangular diagram (CCBC plot). Five different ostracod assemblages were recognized, which with further consideration of the local geology and faunal characters, could be correlated with particular environments of deposition (Dingle 1980).

In the present paper these two techniques are again applied and further modified and extended, with the CCBC plot in particular appearing to hold considerable potential especially when used in conjunction with the distribution of selected species or groupings. Because the oldest sections in the Zululand outcrops are time equivalents of the top part of the BH-9 borehole (Campanian II), it has been possible to extend the well-controlled faunal and ecological classifications of the borehole study to the various outcrops. This gives an excellent 'datum' for palaeoenvironmental predictions in the late Campanian–Maastrichtian rocks in areas of Zululand to the north of the BH-9 borehole.

The ostracod populations from the more isolated outcrops and boreholes in Figure 1 can be compared with the relatively well-known Zululand assemblages, and predictions on their palaeosedimentary environments can then be made. Once the ecological factors have been assessed, some regional and extra southern African biostratigraphic comparisons are attempted.

PALAEOECOLOGY

NORTHERN AREA

BH-9 borehole and Zululand outcrops

Figure 2 shows the sampling localities in this area, and Figure 3 shows the stratigraphic relationships of the various outcrops using Kennedy & Klinger's (1975) ammonite subdivision of the three uppermost stages of the Cretaceous. From these it can be seen that there is likely to be only a slight overlap or possibly a small gap in the succession between the BH-9 borehole and the composite section from outcrop in the Campanian II. This gives a complete section from lower Santonian II to upper Maastrichtian II, including the Santonian-Campanian boundary which occurs between samples at 115 m and 110 m in the BH-9 borehole (Dingle 1980).

In his study of the BH-9 borehole, Dingle (1980) described the Campanian I and II ostracod faunas and allotted them to two ostracod assemblages (4-5) with assemblage 4 appearing 1.5 m beneath the Santonian-Campanian boundary. Applying the same classification, a further two assemblages can be recognized in the Campanian III to Maastrichtian II strata of Zululand, whilst assemblages 4 and 5 can be subdivided.

Ostracod assemblages 4 to 7

54 species assignable to 35 genera have been recorded from the Campanian-Maastrichtian rocks of this area. Their vertical distributions are shown in Table 2, whilst various statistical data on species and population trends through the succession are shown in Figure 67. Two ostracod types numerically dominate the faunas (>20% total population), and in combinations with five other secondary species (each constituting 10-20% total population) and variations in other parameters of the ostracod population (such as similarity, proportion of higher taxa, distribution of minor and rare taxa) allow six distinct groupings within the faunas to be recognized. These assemblages have been annotated 4 to 7, with 4 and 5, as originally defined by Dingle (1980) each subdivided into a and b. Assemblages, with the dominant ostracod types (with maximum %, and mean %, based on 3-point means in parenthesis), are:

Assemblage 4a *Bairdoppilata andersoni* (36%, 27%)

Assemblage 4b *Bairdoppilata andersoni* (36%, 32%)

Assemblage 5a *Bairdoppilata andersoni* (37%, 32%) with *Cytherella* sp. (31%, 28%)

Assemblage 5b *Bairdoppilata andersoni* (41%, 32%) with *Cytherella* sp. (32%, 30%)

Assemblage 6 *Cytherella* sp. (47%, 40%)

Assemblage 7 *Bairdoppilata andersoni* (34%, 32%)

Seven of the rare species are restricted to one or other of these assemblages (see Fig. 67 and Tables 6-7), and certain secondary types, notably *Bythocypris richardsbayensis*, have distributions that allow use to be made of them as assemblage markers. A summary of these associations is given in Table 6.

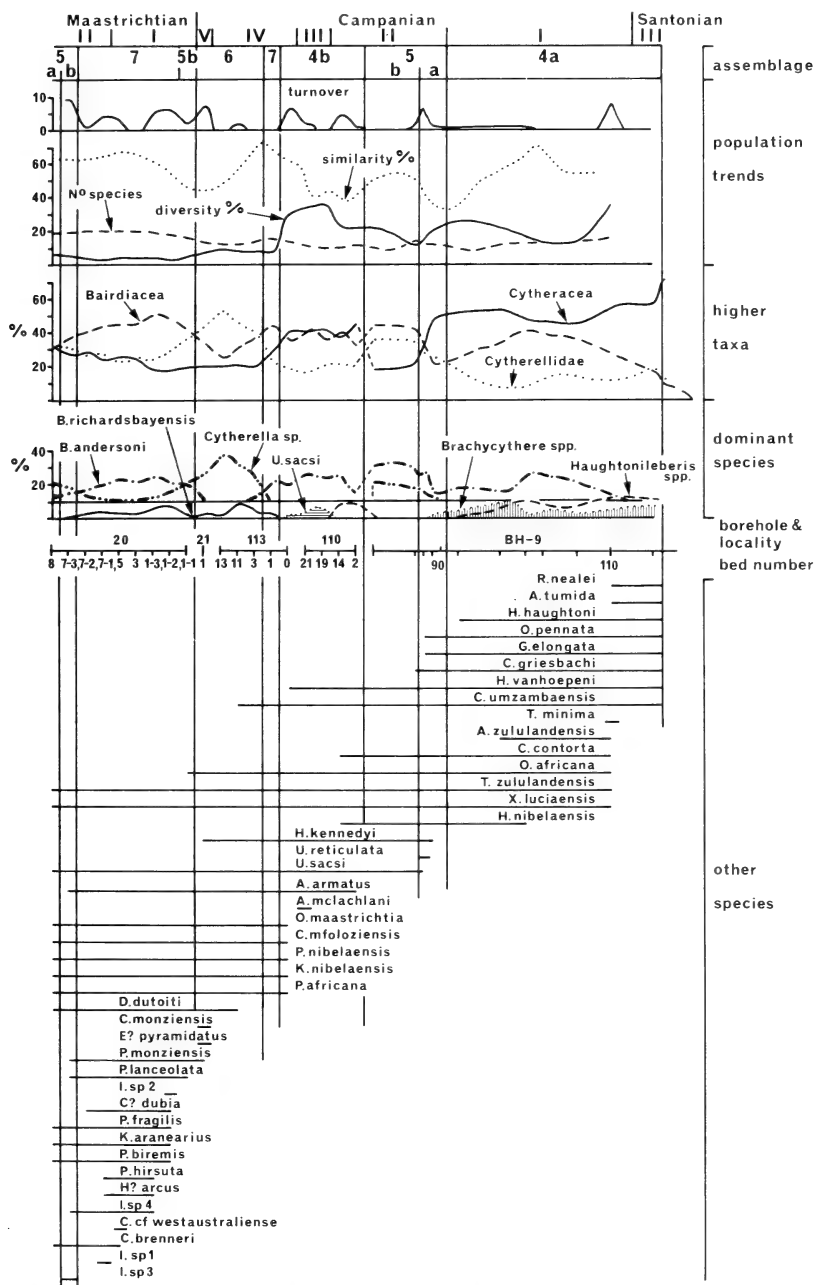


Fig. 67. Variations in the Campanian-Maastrichtian ostracod faunas of Zululand (Richards Bay BH-9 borehole, and outcrops at Nibela Peninsula (locality 110 & 113), Monzi (locality 21), and Mfolozi River (locality 20)). Discontinuities in the various trends have been used to delimit ostracod assemblages 4a, b-7, which are described in detail in the text and summarized in Tables 6 and 9. Population turnover is a measure of the number of new appearances and extinctions in each sample, and population diversity is calculated as number of species per hundred specimens and expressed as a percentage. Population similarity is calculated between adjacent samples in the sequence as number of species common to the two samples/total number of species in both samples $\times 100$. Fluctuations in population similarity will give an assessment of population stability—a sequence of highly similar samples will denote a stable population, and vice versa. Note that in all cases, percentage of species and higher taxa quoted in this figure and in the text are based on three-point running mean values.

P. hirsuta⁺
K. aranearius
C? *dubia*⁺
P. monziensis
P. fragilis

rare (<5%) (1 sample)	O. sp. A.	O. sp. A	O. sp. A
	<i>T. minima</i> ⁺	<i>T. zuluandensis</i>	<i>T. zuluandensis</i>
	<i>T. zuluandensis</i>	<i>C. contorta</i> *	<i>C. mfoloziensis</i>
	<i>C. contorta</i> *	<i>C. mfoloziensis</i>	<i>A. armatus</i>
	<i>A. armatus</i>	<i>H. fissilis</i>	<i>O. africana</i>
	<i>O. africana</i>	<i>K. nibelaensis</i>	
	<i>A. mclachlani</i> ⁺		
	<i>K. nibelaensis</i>		
	<i>G. elongata</i>		
	<i>G. sp. A.</i>		
	<i>P. africana</i>		
	<i>B. longicaudata</i>		
	<i>B. sicarius</i>		
		<i>B. longicaudata</i>	<i>B. sicarius</i>
		<i>C. unzambaensis</i>	<i>C. unzambaensis</i>
		<i>C. klingeri</i>	
		<i>P. fragilis</i>	
		<i>U. reticulata</i> ⁺	
		<i>C. bremeri</i>	<i>C. bremeri</i>
		<i>D. dutoiti</i>	
		<i>C. griesbachi</i>	<i>C. griesbachi</i>
		<i>K. aranearius</i>	<i>K. aranearius</i>
		<i>P. nibelaensis</i>	
		<i>P. biremis</i>	<i>P. biremis</i>
		<i>A. sp. A.</i>	<i>A. sp. A.</i>
		Indet. sp. 3	
		Indet. sp. 4	
		<i>P. monziensis</i>	<i>P. monziensis</i>
		<i>P. lanceolata</i> *	
			<i>H. kennedyi</i>
			<i>H?</i> <i>arcus</i> ⁺
			<i>C. cf. west-</i>
			<i>australienne</i>
			Indet. sp. 1

* restricted to two assemblages + restricted to one assemblage

TABLE 6
Composition of faunal assemblages 4-7 from Campanian-Maastrichtian of Zululand.

assemblage	4a	4b	5a	5b	6	7
Dominant (>20%)	<i>B. andersoni</i>		<i>B. andersoni</i>	<i>Cytherella</i> sp.	<i>Cytherella</i> sp.	<i>B. andersoni</i> <i>Cytherella</i> sp.
Secondary (10-20%)	<i>B. longicaudata</i> <i>H. haughtoni</i> <i>Cytherella</i> sp.	<i>Cytherella</i> sp. <i>H. nibelaensis</i> <i>U. sacsi</i>	none	typically <i>B. richardsbayensis</i>	<i>B. richardsbayensis</i> <i>B. andersoni</i>	<i>B. richardsbayensis</i>
Tertiary (5-10%) (in >1 sample)	<i>B. richardsbayensis</i> <i>B. sicarius</i> <i>H. vanhoepeni</i> * <i>C. klingerii</i> <i>H. fissilis</i>	<i>B. richardsbayensis</i> <i>H. kennedyi</i>	<i>B. richardsbayensis</i> <i>H. kennedyi</i> <i>U. sacsi</i>	<i>H. kennedyi</i> <i>X. luciaensis</i>	<i>C. klingerii</i> <i>X. luciaensis</i>	<i>X. luciaensis</i> <i>O. maastrichtia</i> <i>P. nibelaensis</i> <i>K. nibelaensis</i>
Minor (generally <5%) (>1 sample)	<i>A. tumida</i> <i>A. zuluandensis</i> * <i>H. nibelaensis</i> <i>O. africana</i> <i>C. griesbachii</i> <i>C. umzambaensis</i>	<i>C. umzambaensis</i> <i>H. vanhoepeni</i> * <i>O. maastrichtia</i> <i>X. luciaensis</i> <i>C. klingerii</i>	<i>O. africana</i> <i>O. maastrichtia</i> <i>X. luciaensis</i> <i>H. fissilis</i> <i>B. sicarius</i> <i>B. longicaudata</i>	<i>A. armatus</i> <i>U. sacsi</i> <i>D. dutoitii</i> <i>P. nibelaensis</i> <i>K. mponziensis</i> <i>T. zuluandensis</i>	<i>B. longicaudata</i> <i>U. sacsi</i> <i>D. dutoitii</i> <i>K. mponziensis</i> <i>T. zuluandensis</i>	<i>B. longicaudata</i> <i>A. armatus</i> <i>U. sacsi</i> <i>D. dutoitii</i> <i>K. mponziensis</i> <i>T. zuluandensis</i> <i>P. lanceolata</i> * <i>P. hirsuta</i> * <i>K. aranearius</i> <i>C? dubia</i> * <i>P. monziensis</i> <i>P. fragilis</i>
rare (<5%) (1 sample)	<i>O. sp. A.</i> <i>T. minima</i> * <i>T. zuluandensis</i> <i>C. contorta</i> *	<i>T. zuluandensis</i> <i>C. contorta</i> * <i>C. mfoloziensis</i> <i>A. armatus</i> <i>H. fissilis</i> <i>O. africana</i> <i>A. melachlani</i> * <i>K. nibelaensis</i> <i>G. elongata</i> <i>G. sp. A.</i> <i>P. africana</i> <i>B. longicaudata</i> <i>B. sicarius</i>	<i>O. sp. A.</i> <i>T. zuluandensis</i> <i>C. mfoloziensis</i> <i>K. nibelaensis</i>	<i>T. zuluandensis</i> <i>C. mfoloziensis</i> <i>A. armatus</i> <i>O. africana</i> <i>B. longicaudata</i> <i>C. umzambaensis</i> <i>C. klingerii</i> <i>P. fragilis</i> <i>U. reticulata</i> * <i>C. brenneri</i> <i>D. dutoitii</i> <i>C. griesbachii</i> <i>K. aranearius</i> <i>P. nibelaensis</i> <i>P. biremis</i>	<i>C. umzambaensis</i> <i>C. umzambaensis</i> <i>P. fragilis</i> <i>C. brenneri</i> <i>C. griesbachii</i> <i>K. aranearius</i> <i>P. biremis</i> <i>A. sp. A.</i> Indet. sp. 3 Indet. sp. 4 <i>P. monziensis</i> <i>P. lanceolata</i> *	<i>B. sicarius</i> <i>C. umzambaensis</i>

* restricted to two assemblages

+ restricted to one assemblage

TABLE 7

Species with restricted distribution in the Campanian-Maastrichtian ostracod assemblages of Zululand (BH-9 borehole, Monzi, Mfolozi and Nibela outcrops).

assemblage	4a	4b	5a	5b	6	7	common to
<i>Trachyleberis minima</i>	*						one
<i>Amphicytherura zululandensis</i>	*						
<i>Apateloschizocythere mclachlani</i>		*					
<i>Unicapella reticulata</i>			*				
<i>Curfsina monziensis</i>					*		
<i>Cativella? dubia</i>						*	
<i>Pariceratina hirsuta</i>						*	
<i>Hermanites? arcus</i>						*	
<i>Cytherelloidea contorta</i>	*	*					two
<i>Haughtonileberis vanhoepeni</i>	*	*					
<i>Pterygocythere lanceolata</i>				*		*	
<i>Cytherelloidea griesbachi</i>	*		*	*			three
<i>Haughtonileberis nibelaensis</i>	*	*	*				
<i>Amphicytherura armatus</i>		*		*		*	
<i>Klingerella aranearius</i>		*	*			*	
<i>Cytheropteron brenneri</i>			*	*		*	
<i>Ponticulocythere biremis</i>		*	*			*	
<i>Pedicythere fragilis</i>			*	*		*	
<i>Parvacyptheris monziensis</i>				*	*	*	
<i>Dutoitella dutoiti</i>			*	*	*	*	four
<i>Platella africana</i>		*		*	*	*	

Expressing the make-up of the ostracod populations in terms of a CCBC diagram allows more refined use to be made of the presence and/or absence of certain secondary taxa, as well as bringing out clearly the association of certain minor taxa with particular assemblages (Fig. 69). This is particularly important in the present study where, because of the generally low abundance of the cytheracean component, all the assemblages are dominated by either *Bairdoppilata andersoni* or *Cytherella* sp., a situation that contrasts strongly with the Santonian part of the BH-9 borehole (assemblages 1-3) where the Cytheracea provided the dominant assemblage markers (Fig. 68).

Ostracod assemblages 4 to 7, as defined in Figure 67 and Table 6, plotted on a CCBC diagram (Fig. 68) cluster into well-defined fields in a similar fashion to assemblages 1 to 5 from the Santonian II to Campanian II of the BH-9 borehole (Dingle 1980, fig. 33). Because of the alternating nature of the ostracod assemblages throughout the Campanian II to Maastrichtian II at outcrop (Fig. 67), the CCBC diagram (Fig. 68), in fact, gives a clearer picture of the interrelationships of the various faunas than does a conventional distribution chart (Fig. 67). In the BH-9 borehole, the lowermost Campanian I assemblage (4) was seen to pass rapidly, in the lower part of Campanian II, into assemblage 5, whose field extended progressively towards the CBC baseline. In the present study, populations from the lowermost sections at outcrop (Campanian II)

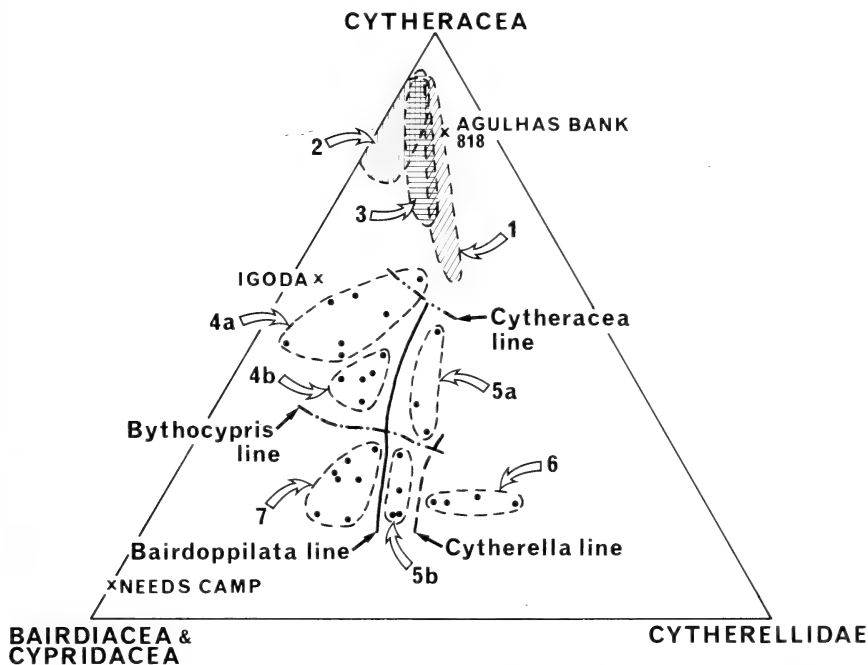


Fig. 68. Triangular (CCBC) plot of Campanian-Maastrichtian ostracod populations from Zululand (Richards Bay BH-9 borehole and outcrops at Nibela Peninsula, Monzi, and Mfolozi River). Individual samples (crosses) from the Agulhas Bank, Igoda, and Needs Camp are also plotted. Assemblage fields 4a, b-7 are delimited by major discontinuities ('Bythocypris', 'Bairdoppilata', and 'Cytherella' lines) which are discussed in the text. The 'Cytheracea' line demarcates areas in which cytheraceans dominate (above) and do not dominate (below). Assemblage fields 1-3 identified in Santonian strata in the BH-9 borehole (Dingle 1980) are shaded.

cluster below the BH-9 assemblage 4 field, yet have very close affinities with it. Similarly, several faunas cluster within the BH-9 assemblage 5 field, yet lie between two other assemblage fields (6-7) that were not encountered in the borehole. Clearly, a redefinition of assemblages 4 and 5 is necessary, but in such a way as to emphasize their internal similarities. Useful in this regard has been the recognition of three important boundaries shown in Figure 68: the 10 per cent (total ostracod) contour of *Bythocypris richardsbayensis* (the 'Bythocypris line'); a line to the left of which *Bairdoppilata* is the dominant ostracod (the 'Bairdoppilata line'); and a line to the right of which *Cytherella* sp. is the dominant ostracod (the 'Cytherella line'). Reference to Figures 68 and 69 shows that the assemblage fields can now be defined in terms of these lines, in addition to other parameters on Figure 67, and Table 6.

A summary of the more important characters of the various ostracod assemblages graphically shown in Figures 67-69 and listed in Table 6 now follows:

Assemblage 4: Bairdoppilata/Brachycythere (4a), *Bairdoppilata/Unicapella* (4b). The whole field of assemblage 4 lies above the 'Bythocypris line' and to the LHS of the 'Bairdoppilata line', with individual cytheracean types making up >10% of the total population. It consists of two clearly defined populations: those of the Campanian I strata of the BH-9 borehole (4a), and those of the Campanian II, III, and IV rocks at outcrop (4b). These can be separated by reference to two parameters:

- (i) the relationship of the Cytheracea and Bairdiacea percentages to the 40 per cent line in Figure 67: in 4a these curves lie above and below the 40 per cent line, respectively; whereas in 4b both fluctuate approximately along the line;
- (ii) the composition of the secondary (10–20%) ostracods types: assemblage 4a (in the BH-9 borehole) has *Brachycythere longicaudata* and *Haughtonileberis haughtoni*, whereas 4b (at outcrop) has *Unicapella sacsi* and *Haughtonileberis nibelaensis*.

As discussed below, we believe that these population differences reflect subtle contrasts in the environmental preferences of the two populations, and are not merely a biostratigraphic phenomenon. It is possible, however, that the differences in character of the minor and rare species between assemblages 4a and 4b (Tables 6–7) reflect the age difference between the two. Five species are restricted to assemblage 4: *Trachyleberis minima* and *Amphicytherura zululandensis* to 4a; *Apateloschizocythere mclachlani* to 4b; and *Cytherelloidea contorta* and *Haughtonileberis vanhoepeni* to 4 (both a and b).

Assemblage 5: Bairdoppilata/Cytherella (5a), *Bairdoppilata/Cytherella/Bythocypris* (5b). The narrow field occupied by assemblage 5 lies between the 'Bairdoppilata' and 'Cytherella' lines, and as such represents a transition between *Bairdoppilata*- and *Cytherella*-dominated fields to the LHS and RHS, respectively. The essential unity of this transitional field can be demonstrated by the distribution of *Hermanites kennedyi* (>20% total cytheraceans), which lies precisely within it, whereas subdivision across the 'Bythocypris line' (5a above, 5b below) identifies populations which have subtle differences at the tertiary and minor taxa levels (Figs 69–70, Table 6)—for examples, the distributions of *Xestoleberis luciaensis*, *Dutoitella dutoiti*, disappearance:appearance ratio in turnover rate, occurrence of blind species, and population similarities.

Only one species is restricted to assemblage 5 (*Unicapella reticulata* to 5a), though six of the other rarer and specialized types occur in either 5a or 5b (Tables 6–7).

Assemblage 6: Cytherella/Bythocypris. The field of this assemblage lies beneath the 'Bythocypris line' and to the right of the 'Cytherella line'. As such, it is the only assemblage in the Campanian–Maastrichtian succession of Zululand in which the genus *Cytherella* completely dominates over *Bairdoppilata* (Fig. 67). Only one species (*Curfsina monziensis*) is restricted to this assemblage which shares other rare and minor forms with assemblages 5 and 7 (Table 7), although their distribution often extends only to the left of field 6 (e.g.

Parvacyptheris monziensis, *Oertliella maastrichtia*, *Hermanites kennedyi*). The only cytheracean ostracod of any numerical significance in assemblage 6 is *Cythereis klinger*, which is rather a curious entrant below the 'Bythocypris line', having earlier in the BH-9 borehole been dominant in the shallow-water, cytheracean-dominated (80–90%) assemblage 3, and only appearing in a tertiary role (5–10%) elsewhere in the Campanian I of assemblage 4a.

Assemblage 7: *Bairdoppilata*/*Bythocypris*. This is the most distinctive ostracod assemblage in the Campanian–Maastrichtian succession of Zululand. On the CCBC diagram (Fig. 68) it lies below the 'Bythocypris line' and to the left of the 'Bairdoppilata line', and is characterized by the presence of a relatively large number of tertiary and minor species (Table 6), most of which reach their maximum development within it (e.g. *Xestoleberis luciaensis*, *Krithe nibelaensis*, and *Oertliella maastrichtia*). In addition, there are several rare cytheracean types, three of which are restricted to this assemblage (*Cativella? dubia*, *Pariceratina hirsuta*, and *Hermanites? arcus*), whilst six others are found in only three other assemblages (Tables 6–7).

Sedimentary environments

In his study of the Richards Bay BH-9 borehole, Dingle (1980) concluded that the various ostracod assemblages reflect specific sedimentary environments of deposition, and for assemblages 4 and 5 predicted the following parameters: moderate-depth (?100–200 m), low-energy, open water; and deep (?200–500 m, outer continental shelf), low-energy, open water, respectively. The present study has confirmed these observations, but additional data on other ostracod assemblages allow further palaeoenvironments to be identified and the definitions of environments represented by 4 and 5 to be modified.

The shallow-water environments of BH-9 borehole (assemblages 1–3) are characterized by a cytheracean component of between 60 and 90 per cent, which drops sharply in the moderate-depth environments of assemblage 4 to between 50 and 60 per cent. A further decrease to less than 30 per cent is evident in crossing the 'Bythocypris line' into the fields occupied by assemblages 5b, 6, and 7 on the CCBC diagram (Figs 67–68). Various authors (e.g. Van Morkhoven 1962; Rosenfeld & Bein 1978) have remarked that a preponderance of smooth-shelled blind genera (e.g. *Bythocypris*, *Bairdoppilata*, *Cytherella*, and *Krithe*) are characteristic of deep-water environments (mid-outer shelf, upper slope), whilst recent work prompted by the Deep-Sea Drilling Programme (e.g. Benson 1977) has corroborated earlier observations (e.g. Brady 1880) that certain of the architecturally complex, typically blind, trachyleberid forms are characteristic components of deep-abyssal populations (mid slope, deep-ocean basin).

The establishment of populations with deep-water (mid-outer shelf, upper slope) aspects accompanies the subordination of the total cytheracean element below the 'Bythocypris line' on the CCBC diagram (Fig. 68). For example, *Krithe nibelaensis*, *Bairdoppilata andersoni*, *Cytherella* sp., *Bythocypris richards-*

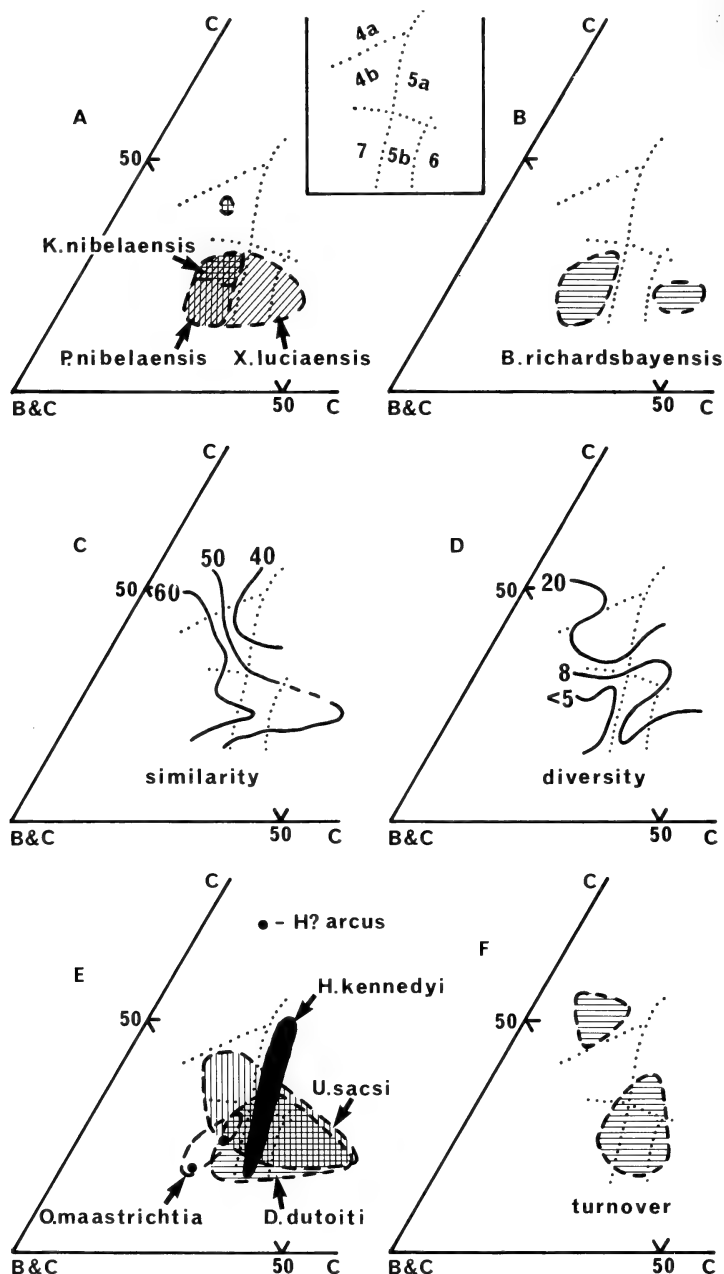


Fig. 69. Various population parameters and species distributions plotted on Cytheracea/Bairdiacea + Cypridacea triangular diagrams. Insert shows assemblage field designations used on Figure 68 and in the text. A. Percentage of total ostracod populations: >5% *Xestoleberis luciaensis* (diagonal lines); >4% *Krithe nibelaensis* (horizontal lines); >5% *Pontocyprilla nibelaensis* (vertical lines). B. >13% total ostracod population *Bythocypris richardsbayensis* (shaded). C. Similarity between adjacent samples in vertical sequence (contour interval 10%). D. Population diversity (contour lines at <5%, 8% and 20%). E. Percentage of total Cytheracea population: >20% *Hermanites kennedyi* (black); >16% *Oertliella maastrichtia* (blank); >10% *Dutoitella dutoiti* (horizontal lines); >9% *Unicapella sacsi* (vertical lines). Two occurrences of *Hermanites? arcus* shown by dots. F. Areas where extinctions dominate over appearances in species turnover.

bayensis, *Pontocyprrella nibelaensis* (all considered typically infra-neritic to bathyal genera by Van Morkhoven (1963)) reach their maximum individual development in the fields of assemblages 5b, 6 and 7 (Fig. 69A–B). *Xestoleberis luciaensis* does the same, although there is no consensus that the genus is a typical deep-water form. Further evidence for deep-water affinities for these assemblages (5b, 6–7) is given by the change in numbers of blind cytheracean species recorded across the 'Bythocypris line' (Fig. 70A, Table 8). Above the line, the number of blind cytheracean species (six) and density of occurrence (an average of one species per sample) is relatively low, whereas below the line, nine species are recorded at an average density of three species per sample. Similarly, architecturally complex cytheraceans such as *Oertliella maastrichtia* and *Hermanites? arcus* cluster below the 'Bythocypris line', whilst *Hermanites kennedyi* occurs above and below the line, but to the right of the 'Bairdoppilata line' (Fig. 69E).

TABLE 8

Distribution of blind cytheraceans in the Campanian-Maastrichtian of Zululand (BH–9 bore-hole, and Monzi, Mfolozi and Nibela outcrops), shown as number of samples containing each species per ostracod assemblage.

	4a	4b	assemblages		6	7
			5a	5b		
<i>Oertliella africana</i>	2	1	1	3		
<i>Trachyleberis zululandensis</i>	1	1	1	2	2	6
<i>Apateloschizocythere mclachlani</i>		1				
<i>Unicapella sacsi</i>		4	2	3	4	6
<i>Dutoitella dutoiti</i>			1	2	3	6
<i>Pedicythere fragilis</i>			1	1		2
<i>Cytheropteron brenneri</i>			1	1		1
<i>C. cf. westaustraliense</i>						1
<i>Pariceratina hirsuta</i>						3
Indet. sp. 2						1
No. of recordings per assemblage	3	7	7	12	9	26
No. of species per assemblage	2	4	6	6	3	8
No. samples per assemblage	7	5	3	4	4	7
No. records per sample per assemblage	0,4	1,4	2,3	3,0	2,3	3,7

The weight of this evidence indicates that the assemblage fields below the 'Bythocypris line' represent moderate to deep-water (mid shelf to upper slope) sedimentary environments. Of these, assemblage 7 probably represents the deepest and most 'specialized', as reference to Table 7 and Figures 67 and 69 shows that it has the highest number of restricted species (three), highest incidence of blind cytheracean types (eight), and is the preferred environment for *Oertliella maastrichtia*, *Krithe nibelaensis*, *Xestoleberis luciaensis*, *Pontocyprrella nibelaensis*, and *Bythocypris richardsbayensis*. In addition, assemblage 7 shows the highest values (typically >60%) in population stability as expressed in terms of percentage faunal similarity (Figs 67, 69C, Table 9), suggesting quiet, physically stable environments, and yet has a very low faunal diversity (<5%)

suggesting somewhat 'hostile' conditions (e.g. cold water, high pressure). On the other hand, abyssal populations, such as those described by Benson (1971), are not evident. This all points to a deep (>500 m) outer continental shelf/upper slope environment.

TABLE 9

Suggested palaeoenvironments and summary of population characters for ostracod assemblages 4-7 in the Campanian-Maastrichtian of Zululand (BH-9 borehole, and Monzi, Mfolozi and Nibela outcrops).

assemblage	4a	4b	5a	5b	6	7
all environments are low—energy, open—water, normal—marine						
palaeoenvironment:	moderate depth (?inner-mid shelf ?100-200 m)	moderate depth (?inner-mid shelf ?200 m) possibly quieter or colder than 4a	moderate depth (mid-outer shelf, ?200-300 m)	deep water (?outer shelf, ?300-500 m)	deep water (?upper slope, > 500 m), unstable (fluctuating currents, temp. etc)	deep water (?upper slope > 500 m) stable
diagnostic ostracoda: > 20%	<i>B. andersoni</i>	<i>B. andersoni</i>	<i>B. andersoni</i> <i>Cytherella</i> sp.	<i>B. andersoni</i> <i>Cytherella</i> sp.	<i>Cytherella</i> sp.	<i>B. andersoni</i> <i>Cytherella</i> sp.
specialized types	<i>H. nibelaensis</i> <i>T. minima</i> <i>A. zululandensis</i>		<i>U. reticulata</i>	none	<i>C. monziensis</i>	<i>C? dubia</i> <i>P. hirsuta</i> <i>H. arcus</i>
other characteristics:						
Cytheracea	50-60%	35-45%	30-50%	20-25%	~20%	20-30%
Bairdiacea	15-40%	30-40%	<40%	>40%	30-40%	40-50%
Cytherellidae	10-20%	10-25%	25-30%	25-35%	40-50%	20-30%
<i>Bythocypris richardsbayensis</i>	<10%	<10%	<10%	usually >10%	>13%	>13%
Faunal diversity	<20% (low)	>20% (high)	~20% (med.)	<20% (low)	<10%	<5%
(number spp/100 spec.)					(very low)	(very low)
Population stability	30-60% (low)	26-63% (low)	37-58% (low)	45-67% (med.)	47-57% (med.)	50-66% (high)
(av. similarity index)						

Assemblage 6 is more difficult to define. Its lower incidence of blind cytheracean species (three), architecturally complex forms, and specialized species (one), as well as its somewhat less stable populations (47-57%), and very low faunal diversity (<10%) suggests a 'hostile', but physically less stable environment than assemblage 7. This evidence can be interpreted as indicating that assemblages 6 and 7 represent geographically similar environments (i.e. both >500 m, outer continental shelf/upper slope), but that assemblage 6 differed in being oceanographically unstable (i.e. subject to more fluctuations in energy of the sedimentary environment, or changes in water temperatures).

Assemblage 5b is intermediate in the sense that it is a pathway for population trends between fields 4b and 6, or 7 and 6. However, characteristics that it shares with 6 and 7, such as the fact that it has the second highest incidence of blind cytheracean species (Fig. 70, Table 8), place it firmly in the 'deep-water' category. No species are restricted to it, and within it the number of specimens of *Bythocypris richardsbayensis* shows a distinct low (>10%, <13%). These features suggest that assemblage 5b represents a somewhat shallower environment than either 6 or 7, an hypothesis strengthened by the

wider range of similarity indices (45–63%) and higher faunal diversity (<20%) than either of the two adjacent fields (Fig. 69C–D, Tables 6, 9). The latter indicates greater ranges of physical parameters than 6 and 7, but less hostile conditions. It is suggested that assemblage 5b represents a quiet, outer-shelf (?300–500 m) environment.

Above the 'Bythocypris line' shallower water conditions are represented by assemblages 4a, 4b, and 5a. Dingle (1980) has discussed the ostracod faunas of assemblage 4a (his 4) and reasoned for moderate-depth, low-energy, inner-mid shelf (?100–200 m) environments. The new data do not contradict this assessment, but necessitate the recognition of a further, closely comparable environment to accommodate assemblage 4b. The two (4a, 4b) have many features in common, for example: the dominance of *Bairdoppilata andersoni*; *Bythocypris richardsbayensis* at <10%; and the presence of individual cytheracean species in secondary abundances (10–20%). They differ, however, in the number of blind species recorded (1,4 species per sample in 4b, and 0,4 species per sample in 4a) and the presence in 4b of the moderate to deep-water species *Unicapella sacs*i and *Hermanites kennedyi*. It is possible that both these types had not evolved in Campanian I times, but coupled with the presence of *Pontocyprrella nibelaensis*, *Oerthella maastrichtia*, *Platella africana*, and *Amphicytherura armatus* in 4b, several of which only appear in large numbers in the deeper water assemblages, the evidence suggests that there is a slightly deeper water element in the 4b faunas compared to 4a. These differences may however, have been controlled by factors only loosely related to depth differences such as quieter water, lower temperatures, lower water turbidity etc., but we have no way at the moment of quantifying them. For the lack of specific data, 4b is tentatively equated with marginally deeper water conditions (?200 m) than 4a (?100–200 m), whilst both represent inner-mid shelf environments.

Assemblage 5a was not distinguished by Dingle (1980) as a separate grouping, but recognition in the present study of the importance of the 'Bythocypris line' necessitates subdivision of assemblage 5 as originally defined. The area above the 'Bythocypris line' (5a) differs in several respects from 5b. In addition to its smaller populations of *Bythocypris richardsbayensis* and *Bairdoppilata andersoni*, there are significantly lower numbers of *Krithe nibelaensis*, *Pontocyprrella nibelaensis*, and *Xestoleberis luciaensis*, and particularly *Dutoitella dutoiti* (which occurs in one sample only). This gives assemblage 5a a distinctly shallower-water aspect compared to 5b. On the other hand, it has certain characteristics in common with 5b which indicate that the two were influenced by similar physical conditions. Notable is the presence of *Unicapella sacs*i and *Hermanites kennedyi*. The latter is an architecturally complex cytheracean whose 20 per cent (total ostracod population) distribution coincides precisely with the 5a and 5b fields. Blind cytheracean types are less important in assemblage 5a than in 5b (2,3 species per sample compared to 3,0 per sample), although both have the same species present. Finally, the population stability within assemblage 5a is lower than within 5b (37–58% compared to 45–67%),

suggesting somewhat less stable physical conditions. 5a is, therefore, considered to be a transitional environment between the moderate depths of field 4 and areas below the 'Bythocypris' line with which it is linked via assemblage 5b. A mid-outer shelf (?200–300 m) environment is suggested.

The concept of field 5 (a and b) as transitional between 4 and 6 and 7 is strengthened by plotting the incidence of species turnover in the CCBC diagram (Fig. 69F). Levels of high turnover, with disappearances predominating, cluster close to the corridor between the 'Bairdoppilata' and 'Cytherella' lines (and also, incidentally, in field 4a). This suggests that certain sedimentary environments (such as 4a and 5) were not conducive to stimulating phylogenetic development (appearances), whereas others (notably 4b) might have been more so.

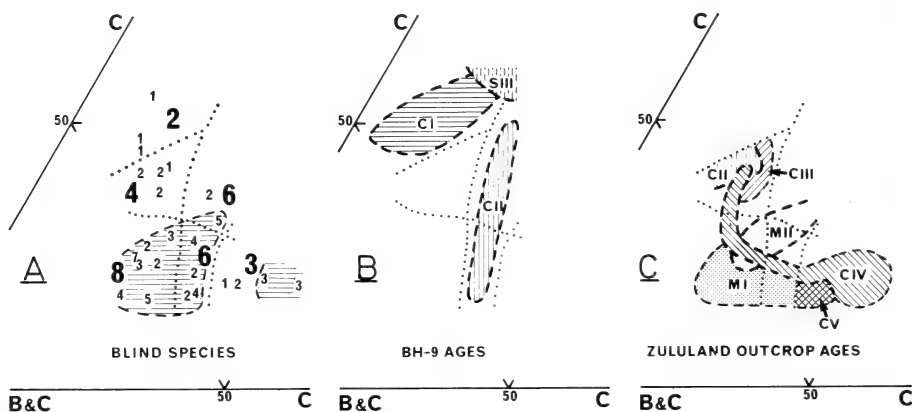


Fig. 70. Population and stratigraphical data plotted on Cytheracea/Cytherellidae/Bairdiacea + Cypridacea triangular diagrams. Assemblage field boundaries shown by dotted lines—designation as in Figures 68 and 69. A. Distribution of blind species of cytheraceans: small figures show numbers of blind species per sample, areas enclosing 3 or more species/sample are shaded; large figures show numbers of different species per ostracod assemblage field. B–C. Ages of samples within ostracod assemblage fields; shading identifies areas enclosing samples of same age; CI = Campanian I, etc. B. Richards Bay BH-9 borehole. C. Zululand outcrops (Monzi/Mfolozi/Nibela).

Having discussed the nature of the ostracod assemblages and the sedimentary environments that they represent, it remains to see how these are distributed in time and space in Zululand. From Figure 67, it is clear that the development of assemblages 4a and 5a, 5b in the Richards Bay BH-9 borehole, and 4b and 5a, 5b at outcrops farther north in Zululand were not synchronous: the moderate to deep-water environments were established earlier in the south (Richards Bay area). These relationships can be graphically presented on the CCBC diagram (Fig. 70B–C), which shows the temporal and spatial distribution of the various sedimentary environments. For example, the occupation of field 4b during Campanian II times in the Zululand outcrops (Fig. 70C) was synchro-

nous with the occupation of field 5 (a and b) farther south at Richards Bay (Fig. 70B). These diagrams also vividly show that for the northerly outcrops there was a change in the sedimentary environments (i.e. migration across the assemblage fields) during the Campanian II to Maastrichtian II interval (approximately 9,4 m.y.) from inner-mid shelf through deep water back to mid shelf (4b to 5a via 6 and 7). Similarly, the change from inner-mid shelf to outer shelf (4a to 5b) during the period Santonian III to Campanian II (approximately 3 m.y.) can be traced in BH-9 (Fig. 70B).

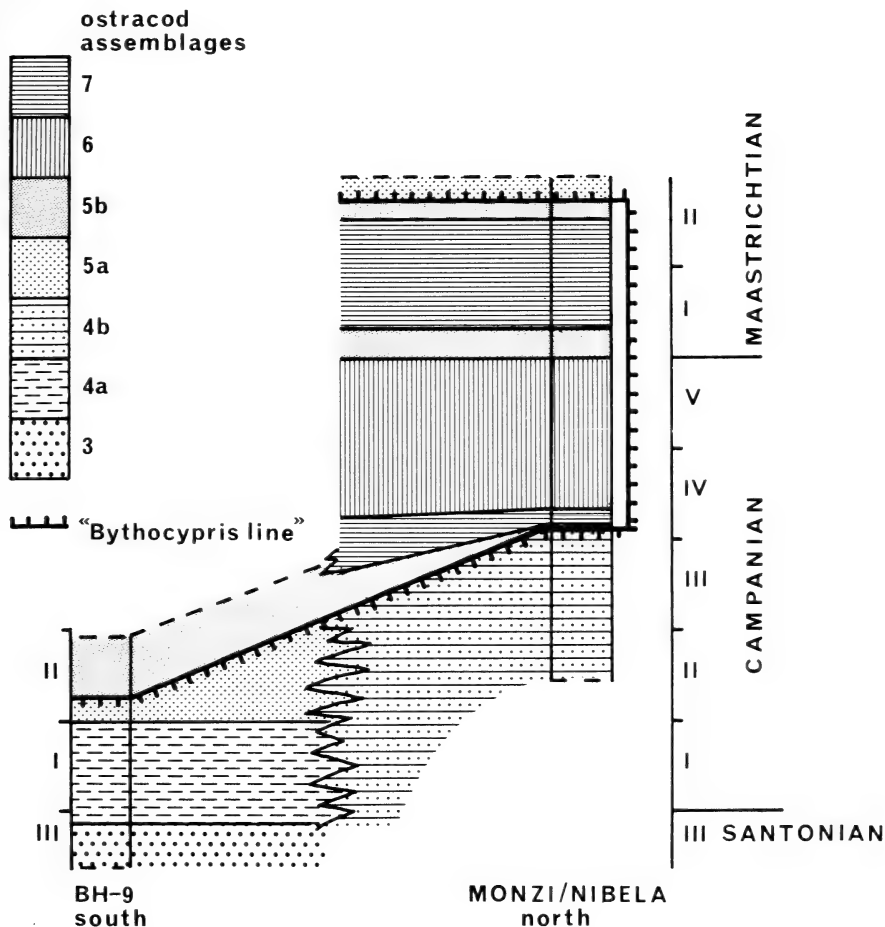


Fig. 71. Temporal distribution of ostracod assemblages in Zululand. Sequence for the northern area is a composite section based on outcrops between the Monzi area (including Mfolozi River) and the Nibela Peninsula. The diagram shows that deep-water assemblages were established earlier in the south, and that the youngest strata in the north indicate a re-establishment of shallower water faunas. These trends are well illustrated by plotting the 'Bythocypris' line.

Lateral correlation of lithostratigraphic units (Fig. 71) between the BH-9 borehole and Zululand outcrops shows that the shallow-water (<100 m), inner and mid-shelf environments (assemblage 4a, 4b) persisted longer in the north, but that the deepening of the water column that followed (in Campanian IV) was very rapid. Because we have no data from the Campanian III to Maastrichtian II section in BH-9, we do not know if a comparable deepening took place in the Richards Bay area, nor if environments such as those represented by ostracod assemblages 6 and 7 were ever established there. The recent review of oil company borehole data from Zululand by McLachlan & McMillan (1979) is too generalized to provide the necessary information.

JC-1 borehole

The JC-1 borehole lies on the continental shelf north-east of Durban on the proximal end of the Tugela delta (cone) (Figs 1, 3, 72). 375 m of Campanian-Maastrichtian sediments were recorded by Du Toit & Leith (1974, fig. 3), who described the sedimentary succession as consisting of monotonous light-grey claystones with thin (<60 cm), hard limestones and subordinate siltstones, and minor very fine-grained sandstones (their lithofacies 5). Stratigraphic control was provided by 'an abundance of planktonic foraminifera' (Du Toit & Leith 1974: 249), and in their summary McLachlan & McMillan (1979, fig. 3) suggest that there is a stratigraphic break at the top of the Maastrichtian in the zones characterized by *Globotruncana contusa* and *G. stuarti*. Du Toit & Leith (figs 4, 6) indicate a coarsening of grain-size and an increase in sedimentation rates (from 18 m/m.y. to 46 m/m.y.) across this hiatus, whereas McLachlan & McMillan (1979) report a decrease in sedimentation rates (47 m/m.y. to 25 m/m.y.) across the Maastrichtian-Palaeocene boundary.

Ostracod faunas

Prior to the present study, no details had been published of the Cretaceous ostracod faunas of the JC-1 borehole, although Dingle (1976) has given a preliminary account of the Tertiary faunas. 28 samples were available for study from the Campanian-Maastrichtian sequence in the borehole, but only 18 contained ostracods: 3 (43%) in the Campanian, and 15 (71%) in the Maastrichtian. The faunas are sparse: a total of 11 species encountered (3 in the Campanian and 11 in the Maastrichtian); no sample contained more than 10 valves, and half contained 2 or less. This distribution contradicts figure 3 in McLachlan & McMillan (1979) which shows the Campanian populations as more abundant than those of the Maastrichtian.

The ostracods and their distribution are shown in Table 10, and the overall impression of the combined Campanian-Maastrichtian populations is of the importance of smooth-shelled, moderately deep-water indicators. In terms of genera, five of the eight identified fall into this category, but in terms of number of valves, their dominance is even more impressive (70%): *Bairdoppilata* 28%, *Bythocypris*? 17%, *Cytherella* 14%, and *Krithe* 11%. Ornamented cytheracean forms (five species) account for only 15 per cent.

TABLE 10

PALAEO- CENE	Bed level, m	<i>Bythocypris</i> ? sp. <i>Krithe</i> sp. <i>Cytherella</i> sp. <i>Bairdopillata</i> cf. <i>africana</i> <i>Australileberis stangerensis</i> <i>Dutoitella mimica</i> <i>Phacorchabdotus</i> ? <i>anomala</i> <i>P</i> ? sp. A <i>Paracypris</i> ? sp. Indet sp. 7 Indet sp. charophytes <i>Inoceramus</i> prisms No. ostracod valves	suggested palaeoenvironments				
MAASTRICHTIAN	1551						
	1570	×	2	1			
	1579			2	?shallow-water, ?restricted environment, essentially barren		
	1597						
	1625	×	×	×	6	2	
	1634					rapid return to moderately	
	1643	×			2	deep water	
	1652	×	×	×	6	(?200 m)	
	1664					3	
	1676		×	×	×	3	?shallow, major, fresh-
	1689		×	×	×	2	water influxes
	1701			×	×	2	
	1719	×	×	×	×	8	4
	1731		×			4	moderately deep water
	1743	×	×			4	(?200 m) evidence of rapid
1756	×	×		×	10	shallowing at top	
1769		×			2		
1780	×				2		
CAMPANIAN	1792					5	
	1811		×	×	×	8	depth gradually increasing
	1823			×	×		upwards to moderate-
	1835		×	×	×	6	water depths (?100-200 m). Establishment of sparse
	1847		×		×	2	ostracod fauna
	1859				×		
	1871			×		2	
	1884		×		×	2	
	1895						6
	1920			×			?shallow water
	1934			×			
SANTONIAN	1945					barren of ostracoda	

Because of the small numbers of specimens encountered, and the very small populations available at any one horizon, it is not possible to recognize assemblages in the same way as in the Zululand area. Nevertheless, some significant associations can be discerned, and these, in descending order down hole, can be summarized as:

- 1 570–1 597 m (uppermost Maastrichtian)—barren, except one carapace of *Bythocypris*?
- 1 625–1 652 m (Maastrichtian)—a *Bythocypris*?/*Krihe* fauna with secondary *Cytherella* and *Bairdoppilata*
- 1 664–1 701 m (Maastrichtian)—a charophytes association with minor ostracod fauna (*Bairdoppilata*, *Australileberis*, indet. sp.)
- 1 719–1 780 m (Maastrichtian)—a mixed *Bythocypris*?/*Krihe*/*Cytherella*/*Bairdoppilata* fauna
- 1 811–1 884 m (early Maastrichtian/late Campanian)—a *Bairdoppilata*/*Cytherella* fauna associated with abundant *Inoceramus* prisms
- 1 895–1 934 m (early Campanian)—barren of ostracods, abundant *Inoceramus* prisms

The rare ornamented cytheracean ostracods occur scattered throughout this sequence and it is difficult to discern a meaningful distribution. It is suggested that the following may be significant: the two records of *Dutoitella mimica* are confined to the 1 811–1 884 m association; the relative abundance of ornamented types in the charophytes-rich horizon 1 664–1 701 m; and the restriction of *Phacorhabdotus*? to associations in which both *Bythocypris*? and *Krihe* are important (1 625–1 652 m and 1 719–1 780 m).

Finally, although ornamented cytheraceans are rare in JC-1, the three identified genera have significant geographical distributions. Most interesting is the presence of two Agulhas Bank Maastrichtian species in JC-1, *Phacorhabdotus*? *anomala*, and *Dutoitella mimica*, which have not been recorded in the near-by Zululand sequences. Similarly, the genus *Australileberis*, which is common in the Eocene of JC-1 and the Agulhas Bank, has been recorded in the Maastrichtian of JC-1, but not from Zululand.

Probably this affinity between the Tugela Cone and the Agulhas Bank (about 1 000 km apart), and the dissimilarity between the ornamented cytheracean elements of JC-1 and south Zululand (130 km between JC-1 and Monzi) reflects contrasting sedimentary environments, although it might have been influenced by palaeoceanographic factors such as currents (i.e. water temperature). Although neither Du Toit & Leith (1974) nor McLachlan & McMillan (1979) give details of the foraminiferal zonation of the Campanian–Maastrichtian, the levels at which *D. mimica* was found (1 911 m Maastrichtian, and 1 871 m Campanian) probably lie stratigraphically below that of sample 818 on the Agulhas Bank (Maastrichtian III), thereby extending its known range to late Campanian to Maastrichtian III.

Sedimentary environments

In addition to the ostracod distribution outlined above, any prediction of the palaeosedimentary environment of the Campanian–Maastrichtian section of the JC–1 borehole must accommodate the following facts: the ostracod fauna as a whole is impoverished; throughout the sequence there is an abundance of authigenic pyrite and agglutinated benthic foraminifera; there is a moderately rich planktonic foraminifera component; ostracod carapaces dominate over single valves. Finally, the general geological setting of the area indicates a location on the top of the Tugela Cone (i.e. a delta top situation) (Du Toit & Leith 1974; Dingle 1976, 1978).

Generally, the sea-floor conditions were not conducive to the establishment of a diverse and abundant ostracod community. This was probably because of the relatively high terrigenous sediment accumulation rate (McLachlan & McMillan 1979), which could account for the abundance of agglutinated foraminifera and the high carapace:single valve ratio, and mildly anoxic bottom waters (giving rise to the authigenic pyrite). On the other hand, the area was in communication, at surface water levels, with the open ocean, thus ensuring a steady influx of planktonic foraminifera. If the association of *Bythocypris*?/*Krithe* is used as an indicator of moderately deep water (?200 m), and the abundance of charophytes is taken to indicate a major influx of fresh water (possibly accompanied by significant shallowing), then the succession of sedimentary environments, as shown in Table 10, can be postulated. This suggests that the period under consideration opened and closed with shallow-water conditions and that there was a further shallow-water episode in 'mid' Maastrichtian times. Periods of deepening and moderately deep water intervened in late Campanian to early Maastrichtian, and in late Maastrichtian times.

This suggests that JC–1 was located in a small delta-top depression, open to the Indian Ocean, but with poor bottom-water circulation. Such an environment was vulnerable to sea-level fluctuations, being delicately balanced between the open ocean on one side and the influence of a major fluvial sediment source on the other. Further implications of the sea-level fluctuations implied by Table 10 will be discussed below.

Campanian–Maastrichtian palaeogeography of southern Natal–Zululand Basin

Because of the upward limit of data in BH–9, we have sufficient information only to construct a Campanian II palaeogeography, although it is unlikely that the overall geography of the southern part of the Natal–Zululand Basin would have altered significantly throughout most of Campanian–Maastrichtian times.

Figure 72 shows a Campanian II reconstruction. To the north of the Tugela delta, the coast was drowned and rugged, with a mountainous hinterland. The sites of BH–9 and the Monzi and Nibela outcrops lay in mid-outer shelf locations, with the shelf edge to the west of the present coast. Although the Campanian II continental shelf was narrow (up to 25 km), it was probably about double the present width and was considerably deeper, ranging from 300–500 m

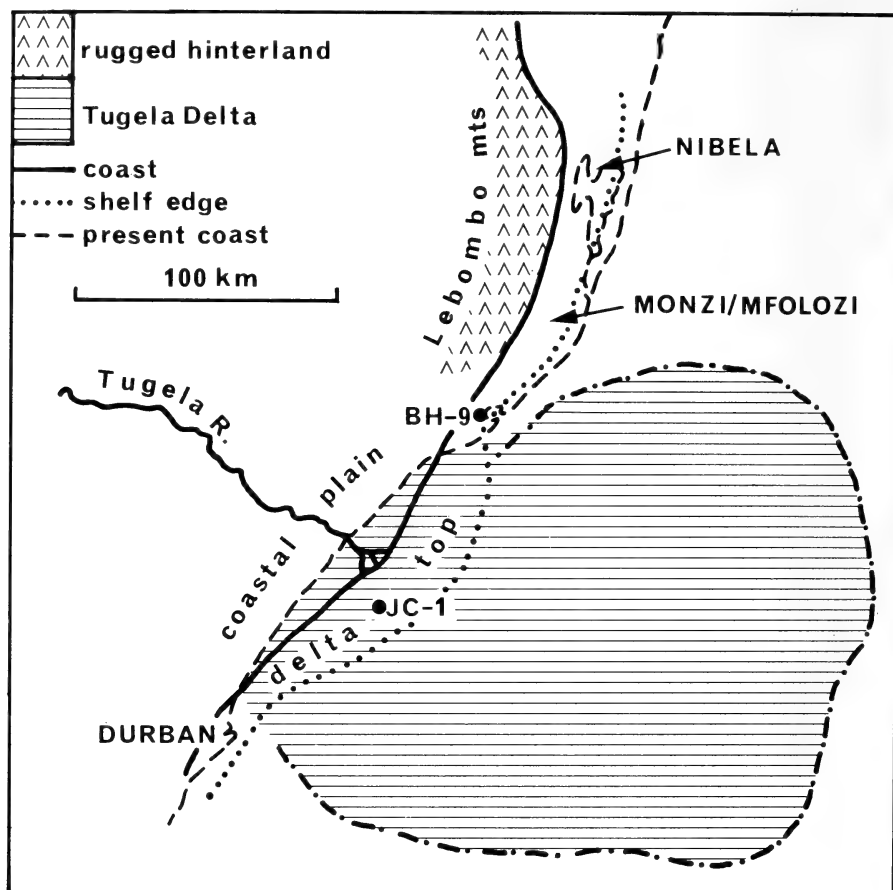


Fig. 72. Campanian II palaeogeography of the Tugela-Zululand area of south east Africa.

in the BH-9 area to ?200 m around Nibela (compared with 50 m today). BH-9 lay about 30 km north of the northern edge of the Tugela delta, which extended as a deep-water cone at least 150 km into the Natal Valley. Immediately south of BH-9, the continental shelf bulged southwards over the delta top, where the site of JC-1 lay in a mid-outer shelf location. We do not have a zonation for the Campanian in JC-1, but from Table 10, Campanian II times probably coincided with shallow-water conditions which were not conducive to an ostracod fauna. The only abundant benthos at this time were benthic foraminifera and *Inoceramus*.

Whilst there are insufficient data to reconstruct further palaeogeographies, it is possible to summarize regional sea-level changes. The most complete data, from BH-9 and Monzi and Nibela, are plotted on Figure 73 as sedimentary environment (related to water depth) versus time. This allows an assessment of

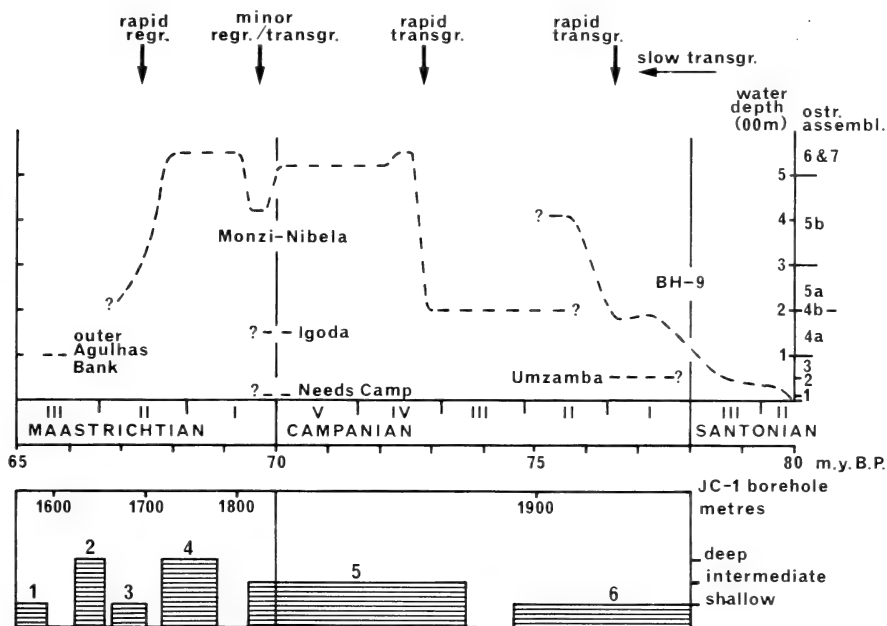


Fig. 73. Sea-level fluctuations in south-east Africa during Santonian II to Maastrichtian II times. Suggested water depths relate to predicted sedimentary environments for ostracod assemblages 1-7 (see Tables 6, 9, and Dingle 1980). Time scale is that of Van Hinte (1976), and ages of Kennedy & Klinger's (1975) ammonite stage subdivisions are nominal. Upper part of diagram relates to Zululand (BH-9 and outcrops between Monzi and Nibela). Single ostracod populations from Igoda, Needs Camp, and Agulhas Bank have been used to predict water depths at these localities for specific times. Lower part of diagram shows suggested temporal distribution of sections 1-6 (shaded) in JC-1 borehole. Table 10 gives details of predicted sedimentary environments for these sections of the borehole.

the spacing and rapidity of the various sea-level fluctuations that affected the area in late Cretaceous times. As noted by several authors (e.g. Kennedy & Klinger 1975; Dingle 1978), the Upper Cretaceous transgression in Zululand is a southward younging phenomenon and the BH-9 succession documents its appearance in the Richards Bay area in Santonian II times. Water depth increase was relatively slow (perhaps 200 m in 3.5 m.y., 57 m/m.y.) through Santonian II to Campanian I times, with a more rapid rise (~133 m/m.y.) in late Campanian I/early Campanian II. Data from the area farther north (Monzi and Nibela) indicate a stand (in this area at a mid shelf, say 200 m depth) for about 3 m.y. during Campanian II to lower Campanian IV times (assemblage 4b), followed by a major, rapid transgression (involving a water depth increase probably in excess of 300 m) in early Campanian IV. A further stand occurred during Campanian IV to lowermost Maastrichtian I (~3 m.y.), with outer shelf/upper continental slope sedimentary environments (assemblages 6 and 7) prevailing in the Mfolozi and Nibela area. A short-lived, minor regression is suspected in Lower Maastrichtian I, which was followed by a minor transgres-

sion that restored deep water (assemblage 7) for a further 1,5 m.y. or so. A major regression started in early Maastrichtian II times, continued evidence for which is found in our youngest samples from south Zululand (mid-upper Maastrichtian II). The data suggest a sea-level fall of at least 200 m over a period of 1 m.y. and this may represent the worldwide end-Mesozoic event, that is locally represented by an uppermost Maastrichtian/early Danian hiatus (Dingle 1978).

No detailed comparison between the sea-level fluctuation curves for Zululand and JC-1 can be made because there is no refined zonation for the latter. However, a rough correlation can be attempted by assuming constant sedimentation rates for the Maastrichtian (56 m/m.y.) and Campanian (12 m/m.y.) sections and plotting the sample levels for JC-1 against the age scale on Figure 73. Several possibly significant points emerge. The basal, barren, ?shallow-water unit (6) correlates with the late Santonian/early Campanian slow transgression/rapid transgression/still stand sequence. The relatively long period represented by unit 5, which shows evidence of a gradual water deepening and the establishment of a sparse ostracod fauna, correlates with the Campanian IV rapid transgression and high sea-level stand in the late Campanian/early Maastrichtian, whilst the short, deep-water episode (4) correlates with the early Maastrichtian high stand. Influxes of charophytes and the general impoverishment of the ostracod fauna in unit 3, which has been tentatively linked with shallow water on the delta top, coincides with the initiation of the rapid mid Maastrichtian regression, but a further short return to moderately deep water in JC-1 (unit 2) has no equivalent in the Zululand succession because no data are available over this time sector. On the Agulhas Bank and in JC-1, the late Maastrichtian was a period of lower sea-levels. Two cautionary notes need to be sounded about these superficially attractive correlations between the Tugela delta top and the continental shelf sites farther north. Firstly, the time scales can be matched only very approximately and, secondly, the two areas were tectonically different—the Tugela Cone subsidence history was long and relatively constant, whereas the Zululand shelf was relatively more stable. Non-eustatic fluctuations may, therefore, have been out of phase and Figure 73 may be comparing different events. On the other hand, this effect could account for the apparent lack of evidence in JC-1 for the rapid early Campanian II transgression, and the smoothing out of the major, rapid Campanian IV transgression. Taken at face value, the sea-level fluctuation histories of the JC-1 borehole, and the Zululand sites show a remarkably good correlation.

EASTERN AREA

Two small outcrops of Upper Cretaceous strata occur south-west of East London. Klinger & Lock (1978) considered the Lower or East Quarry at Needs Camp to represent a shallower water, restricted, lateral facies equivalent of the Igoda Formation, both of which they dated as late Campanian/early Maastrichtian.

Igoda

With its basal conglomerate and rapidly upward fining sequence into sandy limestones and calcareous sandstones, the Igoda Formation represents a transgressive series on to the Palaeozoic–Lower Mesozoic basement of the Transkei Swell. The basal conglomerate contains shell fragments, but all the fossils identified by Klinger & Lock (1978), and the ostracods described herein, came from the calcareous member which lies above the brown conglomerate member. The macrofauna is dominated by ostreid lamellibranchs, whilst other taxa, in descending order of importance are: brachiopods, baculitid ammonites, echinoids, corals, and rare, normally coiled ammonites. The only identifiable macrofaunal element in common between the Igoda Formation and the Umzamba and Zululand areas is *Saghalinites* sp. cf. *S. cala* (Forbes), whilst *Baculites subanceps* Haughton occurs along the west coast of Africa in Angola (Klinger & Lock 1978). The general aspect of the macrofauna suggests moderate to shallow-water depths.

TABLE 11

Ostracods from Igoda Formation (Igoda estuary), late Campanian/early Maastrichtian

		no. specimens	% total
Bairdiacea	<i>Bairdoppilata andersoni</i>	18	19
	<i>B. sp. A</i>	6	6
	<i>Bythocypris richardsbayensis</i>	2	2
Cypridacea	<i>Paracypris umzambaensis</i>	9	12
	<i>P. sp. A</i>	2	
Cytherellidae	<i>Cytherella</i> sp.	4	4
Cytheracea	<i>Cythereis transkeiensis</i>	7	7
	<i>Hermanites kennedyi</i>	4	4
	<i>H?</i> cf. <i>arcus</i>	1	1
	<i>Pondoina igodaensis</i>	14	15
	<i>Hutsonia?</i> sp.	2	2
	<i>Buntonia?</i> sp.	2	2
	<i>Brachycythere longicaudata</i>	14	15
	<i>Xestoleberis luciaensis</i>	2	2
	Indet sp. 5	2	2
	Indet spp	6	6
Dominant (>20%)	<i>Bairdoppilata</i> spp.		
Secondary (10–20%)	<i>Paracypris</i> spp.		
	<i>Pondoina igodaensis</i>		
	<i>Brachycythere longicaudata</i>		
Tertiary (5–10%)	<i>Cythereis transkeiensis</i>		
Cytheracea: total of 54 specimens = 57% fauna			
	Trachyleberididae	26%	
	Brachycytheridae	26%	
	Cytherideidae	26%	
	Progonocytheridae	4%	
	Xestoleberididae	4%	
	Buntoniidae	4%	
	Indet.	10%	

Fifteen species of ostracod belonging to twelve genera have been identified from the calcareous member of the Igoda Formation (Table 11). Cytheraceans are the dominant group (57%), and the assemblage plots on the CCBC diagram close to the BCC line, in the vicinity of assemblage field 4a (Fig. 68). *Bairdoppilata* spp. is the dominant taxa (29%) followed by *Paracypris* spp. (12%), *Pondoina igodaensis* (15%), and *Brachycythere longicaudata* (15%). Two important points of difference between the Igoda population and those of assemblage 4a from the Lower Campanian of the BH-9 borehole are the low level of Cytherellidae (4% at Igoda compared to 10–20%) and the low level of the trachyleberid types (26%). Such low levels of Cytherellidae and Trachyleberidiidae were recorded only in the restricted, shallow-water, high-energy of assemblage 1 of BH-9 (Dingle 1980). As discussed above, field 4a populations are thought to represent quiet, normal marine, moderate-depth (?100–200 m, inner-mid shelf) environments and we consider the Igoda Formation calcareous member was deposited at the shallow (or higher energy) end of this range, i.e. say 100–150 m, inner shelf.

The presence of certain taxa within the Igoda Formation call for further comment. *Pondoina igodaensis* and *Cythereis transkeiensis* indicate a close palaeoenvironmental link with the Santonian–Campanian ostracod populations at Umzamba: although present in south Zululand (BH-9 borehole), the genus *Pondoina* is never common (2–5%), whereas at Igoda and Umzamba it is one of the more important taxa (15% and 10–15%, respectively); similarly, *Cythereis transkeiensis*, which occurs only as a few broken specimens in one sample in the Santonian of BH-9, is relatively important at Igoda and Umzamba (7% and 5% respectively). It is possible that the northern limit of the usual geographical range of *Pondoina* and *Cythereis transkeiensis* lay between Umzamba and Zululand.

Hutsonia? has not been previously recorded from southern Africa, and its environmental preference is usually considered to be brackish to very shallow marine conditions. The presence of a single specimen and the uncertainty of its taxonomic status should caution against too much weight being placed on this record.

Needs Camp, Lower or East Quarry

The sample available for study consisted of a friable to moderately lithified creamish coloured calcarenite. Disaggregation could be only partially achieved and the residues consisted mostly of polyzoa fragments and echinoid spines with abundant red-stained quartz grains. Glauconite grains and benthic foraminifera were common and ostracods rare. No planktonic forams were seen, but they have been reported from the Needs Camp Lower Quarry by McGowran & Moore (1971).

The ostracod fauna was sparse (54 specimens) with a low diversity (<10%) (Table 12). The population is dominated by *Bairdoppilata* (91%), but it is not possible to say whether this is real or a result of the robustness of the recrystallized carapaces allowing this genus to withstand any subsequent decal-

TABLE 12

Ostracods from Needs Camp beds (Lower or East Quarry, Needs Camp),
late Campanian early Maastrichtian.

a. *Present study*

		no. specimens	% total	
Bairdiacea	<i>Bairdoppilata andersoni</i>	39	90	} 94
	<i>B. andersoni aequalis</i>	10		
Cypridacea	<i>Pontocyprrella</i> sp.	2	4	}
Cytheracea	<i>H?</i> cf. <i>arcus</i>	1	2	} 6
	Indet sp. 6	2	4	
Polyzoan calcarenite. Residue consists of polyzoan fragments and echinoid spines, benthic calcareous foraminifera, red quartz and golaucanite				

b. *Ostracoda recorded by Chapman (1916) from Needs Camp Lower Quarry*

	present assignment	S.A. Museum no.
<i>Cythere postcultrata</i> sp. nov.	<i>Cythere? postcultrata</i> Chapman (probably invalid)	2736 18
<i>Bairdia subdeltoidea</i> Münster sp. var. <i>aequalis</i> var. nov.	<i>Bairdoppilata andersoni aequalis</i> (Chapman)	2736 20
<i>Bairdia subdeltoidea</i> Münster	<i>Bairdoppilata andersoni aequalis</i> (Chapman)	2736 17
<i>Bairdia africana</i> sp. nov.	<i>Bairdoppilata africana</i> (Chapman)	2736 19

cification. Chapman (1916) recorded three species of ostracod from this formation, two of which were *Bairdoppilata*, although he did not quote the size of his population. Our population plots on a CCBC diagram well outside any of the other assemblage fields encountered in our studies, which itself is to be expected because the sedimentary environment of this lithofacies (coarse, bioclastic sand) is unlike any other from which we have examined ostracods in the Campanian-Maastrichtian of south-east Africa. Its lithology and invertebrate fauna indicate a very shallow-water (<20 m), normal-marine, moderate to high-energy environment, with coarse carbonate sand substrate.

Comparing the ostracods from the Lower Needs Camp beds with those from the Igoda Formation, the two populations contrast strongly, with the latter having a higher diversity (18% compared to 7%), and a moderately well-represented cytheracean element (12 spp (57%) compared to 2 spp. (6%)). They have in common the dominance of the genus *Bairdoppilata*, and the presence of two species: *Bairdoppilata andersoni*, and *Hermanites?* cf. *H? arcus*. The latter is evidence in favour of, but does not corroborate, Klinger & Lock's (1978) suggestion that the Lower Needs Camp beds and Igoda Formation are the same age, although the macro- and microfaunal evidence indicate that they are both of late Campanian/early Maastrichtian age. Our ostracod evidence does corroborate Klinger & Lock's (1978) suggestion that the Igoda Formation was deposited in deeper water than the Lower Needs Camp beds (see Fig. 73).

Umzamba

The Umzamba Formation at its type section consists of alternating sands, calcareous sands and sandy limestones. Klinger & Kennedy (1977) notated these beds Pi1 to Pi19, and on their ammonite faunas assigned them a Santonian II to Campanian II age (Klinger & Kennedy 1980). These datings have been corroborated by Makrides (1979) using planktonic foraminifera. In the present study two samples were collected from the Campanian I section (beds Pi8 to ?Pi14), but, as found by Makrides in her foraminiferal studies, microfossils in this part of the sequence are sparse and poorly preserved. Table 13 lists the species

TABLE 13

Campanian ostracod faunas from two samples from the Umzamba Cliff section (locality 4 on Figs 1, 3). Bed numbers after Kennedy & Klinger (1977).

Sample from bed Pi 13	no. specimens
<i>Brachycythere longicaudata</i>	5
<i>Bairdoppilata</i> cf. <i>andersoni</i>	2
<i>Amphicytherura tumida</i>	2
<i>Cythereis transkeiensis</i>	fragment
Sample from bed Pi 9	
<i>Brachycythere longicaudata</i>	2
<i>Haughtonileberis fissilis</i>	2

extracted, all of which have previously been recorded from the underlying Santonian III beds by Dingle (1969) and the Santonian III to Campanian I strata in the BH-9 at Richards Bay (Dingle 1980). The main absentees compared with the Santonian III at Umzamba are *Pondoina sulcata* and *Haughtonileberis haughtoni*, whilst a significant presence is *Amphicytherura tumida*, which in Zululand ranges Santonian III to Campanian I. None of the exclusively Campanian or Campanian-Maastrichtian species that first appear in the Campanian I of Zululand has been recorded, but the heavy decalcification to which these beds have obviously been subjected militates against obtaining a representative fauna. With regard to palaeoenvironment, the populations are not suitable for plotting on a CCBC diagram. However, the preponderance of *Brachycythere longicaudata* and *Haughtonileberis fissilis* strongly suggests that they belong in assemblage fields 2 or 3 (<100 m, inner shelf). This in turn suggests that shallow-water conditions persisted in the Umzamba area at least until Campanian I times, when the sea had already deepened to 200 m or more in the Richards Bay area, but had not yet transgressed into the Needs Camp-Igoda region (see Fig. 73).

SOUTHERN AREA: AGULHAS BANK

The presence of uppermost Cretaceous strata on the Agulhas Bank was first established by sea-floor sampling in a slump-exposed outcrop on the upper continental slope (Dingle 1971, 1978). Further dredging and commercial drilling have subsequently shown that Campanian-Maastrichtian rocks occur extensively over the eastern Agulhas Bank in the upper part of the Alphonse Formation (Dingle 1973, 1978; Du Toit 1976; SOEKOR 1976; McLachlan & McMillan

TABLE 14

Ostracods from the Alphard Formation (Agulhas Bank, sample TBD 818), Maastrichtian III.

			no. specimens	% total	
Bairdiacea	.	<i>Bairdoppilata andersoni</i>	3	1	7
	.	<i>Bythocypris richardsbayensis</i>	2	1	
Cypridacea	.	<i>Pontocyprella nibelaensis</i>	8	4	7
	.	<i>Paracypris</i> sp.	2	1	
Cytherellidae	.	<i>Platella africana</i>	1	1	10
	.	<i>Cytherella</i> spp	19	9	
Cytheracea	.	<i>Unicapella sacsi</i>	1	1	83
	.	<i>Dutoitella mimica</i>	21	10	
	.	<i>Phacorhabdodus? anomala</i>	1	1	
	.	<i>Agulhasina quadrata</i>	65	30	
	.	<i>Paraplatycosta reticulata</i>	9	4	
	.	<i>Trachyleberis schizospinosa</i>	73	33	
	.	<i>Parvacyptheris spinosa</i>	7	3	
	.	<i>Krithe nibelaensis</i>	2	1	
	<i>Apateoschizocythere laminata</i>	5	2		
Dominant (>20%)			<i>Trachyleberis schizospinosa</i>		
			<i>Agulhasina quadrata</i>		
Secondary (10–20%)			<i>Dutoitella mimica</i>		
Tertiary (5–10%)			<i>Cytherella</i> sp.		
Cytheracea: total of 184 specimens			= 84% fauna. Trachyleberididae = 96%		

1979; Klinger *et al.* 1980). So far, however, the only description of their ostracod fauna is that given by Dingle (1971) of sample TBD 818 (Figs 1, 3) which is of upper Maastrichtian (probably Maastrichtian III) age.

15 species of ostracod, assigned to 15 genera have been identified from sample 818 (Tables 1, 14), and of these, 9 genera (60% by number of species, 18% by number of specimens) have been recorded from the Campanian–Maastrichtian of Zululand. The fauna is overwhelmingly cytheracean (83%) with *Trachyleberis schizospinosa* (33%) dominant, and *Dutoitella mimica* (10%) in a secondary role. On a CCBC diagram (Fig. 68) the population of sample 818 lies adjacent to the field of assemblage 3, as defined in BH–9, but in several ways the population make-up of 818 differs significantly from those of assemblage 3. In addition to specific differences accountable by the age difference, 818 contains a small number of Bairdiacea (which assemblage 3 does not), a higher percentage of Cytherellidae (10%) than most of the assemblage 3 populations, whilst the genera *Krithe* (1%), *Unicapella* (1%), *Dutoitella* (10%), and *Trachyleberis* (33%), which are all absent from assemblage 3, are typically moderate to deep-water taxa. Furthermore, five species of the nine cytheraceans in sample 818 are blind forms, and numerically blind forms make up 88 per cent of the cytheracean population (Table 14). In contrast, only one blind cytheracean type occurs in assemblage 3 (*Rayneria nealei*, which is a minor constituent, up to 7%). The trachyleberid component of the cytheracean fauna

in sample 818 is 93 per cent (number of specimens), which is higher than in any other sample from the Campanian–Maastrichtian rocks of south-east Africa. Significantly, however, the next highest values recorded (76%, mean of 6 samples) were from the populations of assemblage 3.

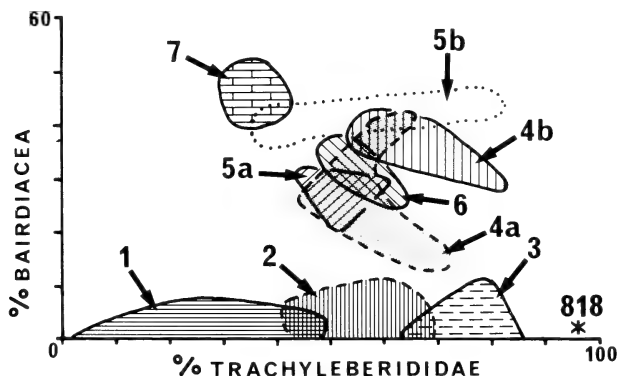


Fig. 74. Fields for ostracod assemblages 1–7 on a percentage Bairdiacea (total fauna) v. percentage Trachyleberididae (of Cytheracea) plot. Sample 818 from the Agulhas Bank lies near the Bairdiacea baseline, on the RHS of the diagram. See text for explanation.

Contrasts with typical populations in assemblage 3 makes the assessment of a palaeosedimentary environment for sample 818 uncertain. Despite the differences mentioned above, however, the overall composition of the population of sample 818 places it firmly within the shallow-water area of the CCBC diagram. Nevertheless, the overwhelming blindness of the fauna and the presence of elements which are typically indicators of deeper water show that sample 818 was not deposited in a near-shore or even mid-shelf environment, as were the assemblage 3 populations in the BH–9 borehole. This uniqueness can be further emphasized by comparing the trachyleberid percentage of the Cytheracea of all the Zululand Santonian–Maastrichtian samples to some parameter that is independent of the cytheracean component, such as the Bairdiacea percentage. Figure 74 shows a progressive increase in the trachyleberid component of the Cytheracea with increase in water depths and open oceanic influences up the BH–9 borehole to a point where moderate water depths replace shallow ones. Movement of the assemblage fields representative of deeper-water environments is in the reverse direction, with the bulk of the deep-water assemblages (5b, 6 and 7) lying to the left of the 60 per cent trachyleberid value, and showing a general decrease in trachyleberid values with an increase in Bairdiacea percentage. Sample 818 lies in the shallow-water areas, but well to the right of other assemblage 3 populations, indicating what may be termed a ‘modified assemblage 3 sedimentary environment’.

Although the evidence is inconclusive, we suggest a quiet, shallow-water environment (as for assemblage 3), but with dominant open-ocean influences.

Considering the geographical position of sample 818 (in the vicinity of the Upper Cretaceous shelf break where the shelf is about 135 km wide), this suggests an outer shelf/upper slope setting in shallow water (?~100 m). Such an unusual sedimentary environment was presumably created during a regression that may be correlated with the major regression that we have identified as commencing in Maastrichtian II in our Zululand samples (Fig. 73).

SUMMARY

Within the context of the continental shelf and upper slope environments encountered in the Santonian–Campanian–Maastrichtian of south-east Africa, it is possible to summarize the palaeosedimentary environments of the ostracod faunas studied in terms of a CCBC diagram. The various fields* (assemblages 1–7, as shown in Figure 68), as well as the data from isolated samples from Needs Camp, Igoda and the Agulhas Bank are shown in Figure 75. Environments deeper than 100 m (i.e. mid-shelf and deeper, assemblage fields 4–7) lie in the central part of the diagram, with the deeper-water areas (assemblages 5b, 6 and 7) lying towards the CBC base line (i.e. below the 30% Cytheracea line). The anti-clockwise closure of the 100 m line in the high Bairdiacea/Cypridacea populations is somewhat speculative and is based on the Needs Camp populations.

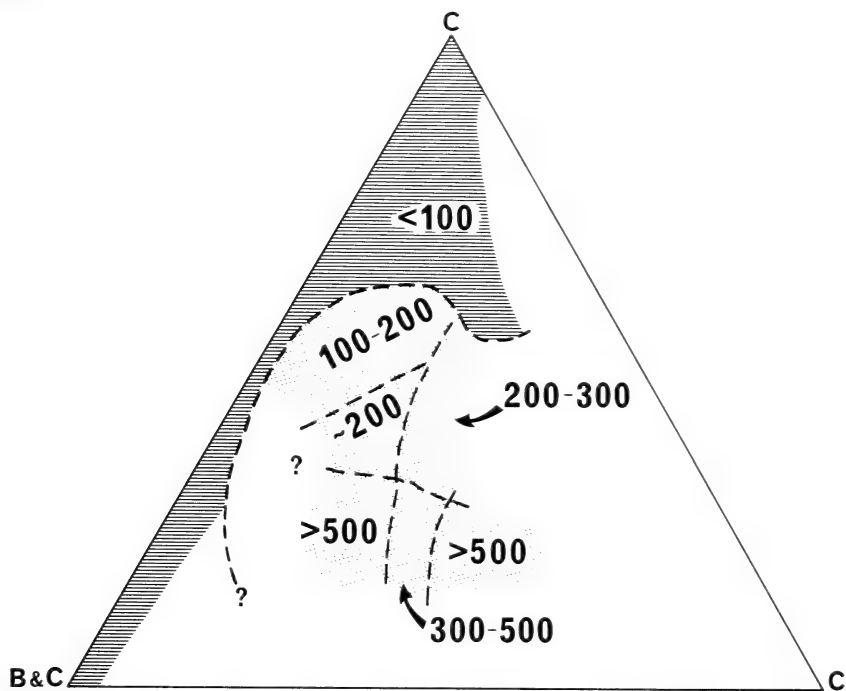


Fig. 75. CCBC triangular diagram used to predict depths (in metres) of palaeosedimentary environments of ostracod assemblages in the Campanian–Maastrichtian strata of south-east Africa. Constructed from Figure 68 and Table 6, it includes data from Zululand, Igoda, Needs Camp, and Agulhas Bank. Within the dotted areas (>100 m depth), the field boundaries are those shown in Figures 68 and 69 (insert). See text for explanation.

Large areas, especially within very low value cytheracean populations, as well as high Cytherellidae populations are completely unknown, but in conjunction with Tables 6 and 7 it is hoped that Figure 75 will prove of use in future studies in discriminating palaeosedimentary environments in pre-Santonian south-east African sequences where more extensive shallow-water environments are anticipated. Clearly, Figure 75 will be ineffective in abyssal populations where an 'overlay' for such environments will need to be made.

BIOSTRATIGRAPHY

SOUTH-EAST AFRICA

Because of the relatively limited spatial distribution of individual species, benthic ostracods are not used in worldwide stratigraphic zonal schemes. They can, however, be effective locally, and several notable attempts have been made to extend zonation over moderate-sized regional studies (e.g. Simon & Bartenstein 1962; Oertli 1963). Data on the temporal distribution of species can be grouped in various ways to highlight the evolution of local ostracod faunas, and three of the most useful of these have been effectively employed in a recent survey of the British Phanerozoic ostracods (Bate & Robinson 1978): phylogeny emphasizing first appearances of individual species (which illustrates the evolution of the faunas as a whole), phylogeny emphasizing extinctions of individual species (the method of plotting 'tops' of species ranges), and generic phylogeny. Only in the Zululand area do we have sufficient data to attempt a similar study, although the faunas from Agulhas Bank and Transkei Swell outcrops can be compared individually. Figures 67, 76–80 show data on the Campanian–Maastrichtian ostracod faunas in Zululand plotted in the three modes mentioned above to emphasize their biostratigraphic distribution.

Phylogeny: species distribution (appearances)

Firstly, we shall look at the overall temporal population trends using the stage subdivisions of Kennedy & Klinger (1975) as reference points. It is clear from a comparison of Figures 67, 76–77 and Table 15, that the response to environmental change was largely accomplished by changes in the proportions of the various species present, rather than wholesale invasion or withdrawal of large numbers of different types. For instance, the similarity between the species composition of stage subdivisions in the Campanian I to Maastrichtian II sequence does not fall below 60 per cent, and rises steadily through the Campanian from 61 per cent between Santonian III and Campanian I to 77 per cent between Campanian IV and Campanian V (Fig. 76, Table 15). This is despite the fact that several of the subdivisions (Campanian IV for example) contain populations that represent sedimentary environments ranging from moderate depth inner-mid shelf (assemblage 4b) to deep-water outer shelf/upper continental slope (assemblages 6–7). This basic continuity in species presence is further borne out by the curve which plots percentage of species in a stage

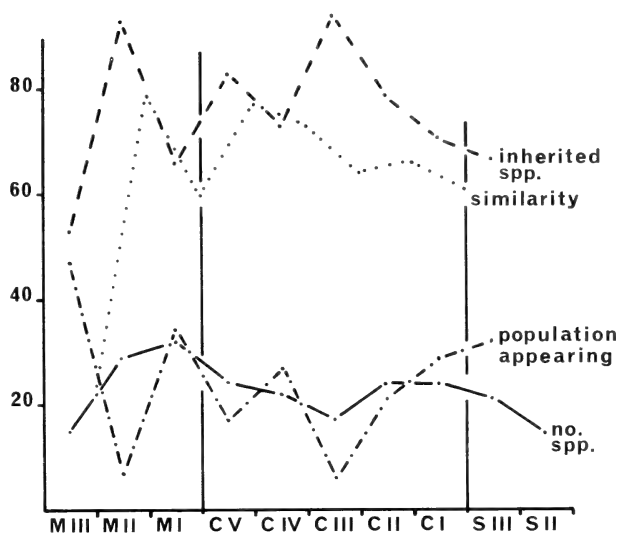


Fig. 76. Ostracod population trends plotted by stage subdivision in Santonian II to Maastrichtian III of Zululand and Agulhas Bank. Curves for inherited species, similarity, and population appearing (residual of inherited species curve) are expressed as percentages of total ostracod populations. Number of species extant is given for total ostracod population. Data from Figure 77. See text for discussion.

TABLE 15
Biostratigraphic data (species distribution) on Campanian-Maastrichtian ostracoda from Zululand (BH-9, and Monzi, Mfolozi and Nibela) and Agulhas Bank.

	Sant. III	Camp. I	Camp. II	Camp. III	Camp. IV	Camp. V	Maas. I	Maas. II	Maas. III
no. species extant	21	24	24	17	22	24	32	29	15
inherited (%)	14 (67)	17 (71)	19 (79)	16 (94)	16 (73)	20 (83)	21 (66)	23 (93)	8 (53)
restricted (%)	1 (5)	2 (8)	2 (8)	1 (6)	0	2 (8)	2 (6)	2 (10)	7 (47)
appearances (% total)	7 (32)	7 (29)	5 (21)	1 (6)	6 (27)	4 (17)	11 (34)	2 (7)	7 (47)
disappearances (% total)	4 (19)	5 (21)	8 (33)	1 (6)	2 (9)	3 (13)	5 (16)	21 (72)	?
<i>Similarity</i>									
no. species	28	29	25	22	26	35	34	36	
common species	17	19	16	16	20	21	27	8	
% similarity	61	66	64	73	77	60	79	22	
no. species		45				60			
common species		17				21			
% similarity		Sant./Camp. similarity 37%			Camp./Maas. similarity 35%				
no. species extant	22		40				41		
inherited (%)	?		17 (43)				21 (51)		
restricted (%)	?		10 (25)				20 (49)		
appearances (% total)			23 (58)				20 (49)		
disappearances (% total)			19 (48)				at least 26 (>63%)		

subdivision inherited from the subdivision below (Fig. 76)—a steady increase from Santonian III (67%) to between 83 and 94 per cent in Campanian III to Campanian V—and is matched by low values (10–30%) for species restricted to one stage subdivision, and the low number of species (ten, 18%) that are restricted to two or less of the various ostracod assemblages.

The largest decline in similarity and inherited species content, and the main event that is the exception to the general trend outlined above, occurs across the Campanian–Maastrichtian stage boundary (Fig. 76), where both values fall from 80 per cent to around 60 per cent, and then climb rapidly to their former values higher in the Maastrichtian. This discontinuity is caused by the appearance of a relatively large number of new species (~30%) that is not accompanied by any marked change in the overall rate of extinction (~15%). It is likely that several of these species, which give assemblage 7 its characteristic composition, represent special types that became established in response to stable, deep-water conditions and whose local 'extinction' followed the reversion to shallower environments in Maastrichtian II (Figs 67, 77). In all probability, therefore, the local temporal ranges of species such as *Pariceratina hirsuta*, *Hermanites? arcus*, *Cytheropteron* cf. *westaustraliense*, indet. sp. 2, and *Cativella? dubia* do not reflect their 'absolute' temporal ranges, i.e. they represent a facies fauna. On the other hand, some of the new species that established themselves early in Maastrichtian I did not become extinct with the re-establishment of assemblage 5a, 5b and these types (e.g. *Klingerella aranearius*, *Pedicythere fragilis*, *Ponticulocythere biremis*, and *Cytheropteron brenneri*) may, therefore, be more age diagnostic than the former, short-range group. Species in the Campanian whose short ranges and associations with particular assemblages similarly suggest strong environmental control, and therefore lessen their use biostratigraphically, are *Trachyleberis minima* (Campanian I), *Unicapella reticulata* (Campanian II), and *Curfsina monziensis* (Campanian V).

In line with the high percentage species similarities between stage subdivisions, the percentage similarity between stages is stable, decreasing only very slightly up the succession—Santonian/Campanian 37%, Campanian/Maastrichtian 35%—with 58 per cent of the Campanian species appearing within that stage compared to 49 per cent in the Maastrichtian.

One notable feature of Table 15 is the increase in number of species per stage from 22 in the Santonian to 41 in the Maastrichtian. Plotted by stage subdivision (Fig. 76), this increase has two peaks: Campanian I and II (24) and Maastrichtian I (32), with an intervening low (16) in Campanian III which follows a high in species extinction (30%) in Campanian II and from which the faunas did not start to recover until Campanian IV. Whether this phenomenon is environmentally controlled, or reflects overall phylogeny is not known, but it is a point we shall return to later.

Of the total number of species in the Campanian–Maastrichtian strata of Zululand and the Agulhas Bank (60), 17 are inherited from the Santonian III, 10 are restricted to the Campanian, 20 restricted to the Maastrichtian, and the

remaining 13 restricted to Campanian–Maastrichtian. The ranges of these are shown in Figure 77, on the left of which are plotted the species inherited from the Santonian III. There is a sharp decrease in the numbers of these species in Campanian II (four become extinct), but thereafter their numbers show a slow but steady decline so that four only are known to extend above Maastrichtian II.

Of the 10 species restricted to the Campanian, 7 had appeared by the end of Campanian II, and of the 20 restricted to the Maastrichtian, 11 had appeared by the end of Maastrichtian I. The curve showing number of appearances as a percentage of total population (which is a residual of the 'inherited species' curve, Fig. 76) gives an assessment of evolutionary activity. It can be seen that whilst the Maastrichtian I was marked by an evolutionary 'burst' (33%), the early part of the Campanian seems to have been part of a downward cycle from Santonian III (32%) that reached a low of evolutionary activity (6%) in the Campanian III.

Ostracod zonal scheme

It is accepted as sound stratigraphic policy to establish, wherever possible, local biostratigraphic zonal schemes that are based on benthic organisms, but that can be tied in with an established regional zonation based on planktonic and/or nektonic taxa (such as ammonites, planktonic foraminifera etc). A prime justification for this is that it frequently allows a good assessment of age to be made in other local lithofacies in which the internationally accepted zonal fossils are absent or poorly preserved. Using the distribution of the ostracod taxa in Zululand, and selecting species which, as far as possible, show palaeo-environmental tolerance, we propose an ostracod zonal scheme for south-east Africa. The zonal boundaries are shown on Figures 77–78, and 80 and the zones defined below. Kennedy & Klinger's (1975) ammonite zonations are used as a framework for the scheme. It should be noted that in the following definitions only particularly characteristic associations are mentioned, and that the complete associations can be identified from Figure 77. The locality numbers given below are after Kennedy & Klinger (1975).

***Amphicytherura zululandensis* Zone**—range lower and middle part of Campanian I. *Definition*: period defined on presence of index species *Amphicytherura zululandensis*. *Remarks*: the lower part carries the association *Rayneria nealei*, *Amphicytherura tumida*, and *Cytherelloida contorta* with *Amphicytherura zululandensis*. In the upper part, the associated ostracods are *Haughtonileberis haughtoni*, *H. nibelaensis* and *Oertliella africana*. So far recognized entirely from strata within the BH-9 borehole.

Un-named Zone—range uppermost Campanian I. *Definition*: period between the last appearance of *Amphicytherura zululandensis* and the first appearance of *Hermanites kennedyi*. *Remarks*: no short-ranging species have been identified in this period, which includes the top of the range of *Haughtonileberis haughtoni*. So far recognized entirely from strata within the BH-9 borehole.

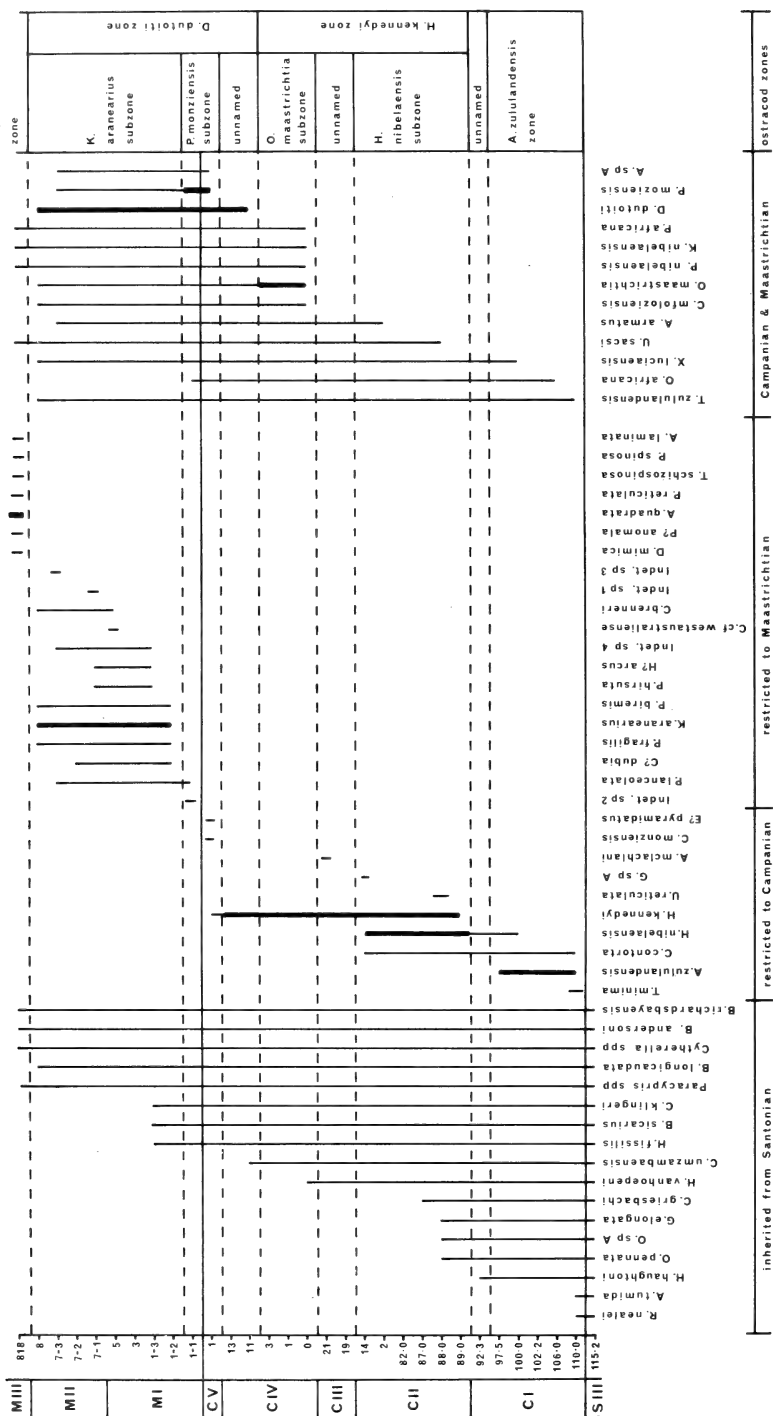


Fig. 77. Temporal distribution of ostracod species in Campanian-Maastrichtian strata of Zululand (BH-9, and Monzi, Mfolozi and Nibela outcrops) and Agulhas Bank. Species grouped according to their distribution. Left-hand column gives Kennedy & Klinger's (1975) ammonite subdivisions, and sampled bed numbers (see Table 1 and Figs 3 and 67). Right-hand column gives ostracod zonation proposed herein. Thickened range bars show species used for zonal purposes.

***Hermanites kennedyi* Zone**—range Campanian II to middle Campanian IV. *Definition*: period which begins with first appearance of *Hermanites kennedyi* and ends with the first appearance of *Dutoitella dutoiti*. *Remarks*: can be divided into three subzones and has been recognized in strata from the BH-9 borehole and at outcrops in Nibela Peninsula (localities 110 and 113).

***Haughtonileberis nibelaensis* Subzone**—range Campanian II. *Definition*: period marked by the presence of *Hermanites kennedyi* and *Haughtonileberis nibelaensis*. *Remarks*: the lower part carries the association of *Oertliella pennata*, *Uncapella reticulata*, and *Haughtonileberis vanhoepeni* with *Haughtonileberis nibelaensis* and *Hermanites kennedyi*. The middle and upper parts carry the association *Uncapella sacsi* and *Haughtonileberis vanhoepeni* with *Hermanites kennedyi* and *Haughtonileberis nibelaensis*. Recognized in the BH-9 borehole and at outcrop on the Nibela Peninsula (locality 110).

Un-named Subzone—range Campanian III. *Definition*: period marked by the presence of *Hermanites kennedyi* between the last appearance of *Haughtonileberis nibelaensis* and the first appearance of *Oertliella maastrichtia*. *Remarks*: no short-range species have been identified in this period which includes the upper part of the range of *Haughtonileberis vanhoepeni* and the one record of *Apateloschizocythere mclachlani*. Recognized at outcrop on the Nibela Peninsula (locality 110).

***Oertliella maastrichtia* Subzone**—range early and middle part of Campanian IV. *Definition*: period marked by the presence of *Hermanites kennedyi*, beginning with the first appearance of *Oertliella maastrichtia* and ending with the first appearance of *Dutoitella dutoiti*. *Remarks*: the lowermost part of this zone coincides with the appearance of several new species: *Pontocyprrella nibelaensis*, *Krithe nibelaensis*, *Platella africana*, which form a distinctive association with *Hermanites kennedyi* and *Oertliella maastrichtia*. Recognized at outcrop on the Nibela Peninsula (locality 113).

***Dutoitella dutoiti* Zone**—range late Campanian IV to early Maastrichtian II. *Definition*: period defined on the presence of index species *Dutoitella dutoiti*. *Remarks*: can be divided into three subzones, and has been recognized at outcrop on the Nibela Peninsula (locality 113), in the Monzi road section (locality 21) and along the Mfolozi River (locality 20).

Un-named Subzone—range upper Campanian IV. *Definition*: period marked by the presence of *Dutoitella dutoiti* and *Hermanites kennedyi* that begins with the first appearance of *Dutoitella dutoiti* and ends with the first appearance of *Parvacythereis monziensis*. *Remarks*: carries the association of *Hermanites kennedyi*, *Dutoitella dutoiti* and *Oertliella maastrichtia*. Recognized at outcrop on the Nibela Peninsula (locality 113).

***Parvacythereis monziensis* Subzone**—range Campanian V to early Maastrichtian I. *Definition*: period marked by the presence of *Dutoitella dutoiti* and *Parvacythereis monziensis* that begins with the first appearance of *Parvacythereis monziensis* and ends with the first appearance of *Klingerella aranearius*.

Remarks: carries the association of *Dutoitella dutoiti* and *Parvacyptheris monziensis*. In addition, in the lower part (Campanian V) it includes the uppermost range of *Hermanites kennedyi* as well as the typical Campanian V species *Curfsina monziensis*. The early Maastrichtian I part sees the appearance of *Pterygocythere lanceolata* and the extinction of *Oeriliella africana*. Recognized at outcrops in the Monzi road section (locality 21) and along the Mfolozi River (locality 20).

***Klingerella aranearius* Subzone**—range middle Maastrichtian I to late Maastrichtian II. *Definition:* period defined by the presence of index species *Klingerella aranearius*, together with *Dutoitella dutoiti*. *Remarks:* this zone, whose top cannot at present be located precisely, is typified by rich and varied faunas that include the association of *Pterygocythere lanceolata*, *Ponticulocythere biremis*, *Pariceratina hirsuta*, and *Hermanites? arcus*, with *Klingerella aranearius* and *Dutoitella dutoiti*. Recognized at outcrop along the Mfolozi River (locality 20). For a finer subdivision of the Maastrichtian strata it would be desirable to erect further subzones at the top of the *Dutoitella dutoiti* zone (i.e. to shorten the *Klingerella aranearius* subzone). This may be possible with further work, but at present all the short-range species available (e.g. *Cytheropteron* spp., indet spp. 3 and 4) are either too poorly known, or seem too environmentally-bound to be suitable.

***Agulhasina quadrata* Zone**—range ?Maastrichtian III. *Definition:* period defined on the presence of index species *Agulhasina quadrata*. *Remarks:* the rich and varied cytheracean assemblage of *Agulhasina quadrata*, *Dutoitella mimica*, *Trachyleberis schizospinosa*, *Paraplatycosta reticulata*, and *Phacorhabdotus? anomala* is typical of a zone whose top and bottom cannot yet be precisely defined. Recognized at outcrop on the sea-floor of the outer Agulhas Bank (locality 818).

Phylogeny: higher taxa

Figure 78 and Tables 16 and 17 reveal that, although the Cytheracea are numerically dominant only in Campanian I (Fig. 67), they are the most diverse group both in species and genera throughout the Campanian and Maastrichtian, and that they show considerable evolutionary activity during the last 13 m.y. of the Cretaceous in south-east Africa. Expressing this in terms of distribution and appearance of new species by family (Table 17a), the Trachyleberididae are seen to be the most diverse and phylogenetically active family within the Cytheracea. This diversity is greatest in Campanian II, where the number of species belonging to the Trachyleberididae reaches 82 per cent of the cytheracean component (Fig. 79). This value falls steadily to 42 per cent in Maastrichtian II, indicating a relative reduction in evolutionary activity within the family in progressively younger strata. (The sharp rally to 67 per cent in Maastrichtian III is based on one sample only and cannot be taken as representative.) This decline in phylogenetic activity within the Trachyleberididae is also evident if the figures for number of species appearing per stage (expressed as a percentage of the total

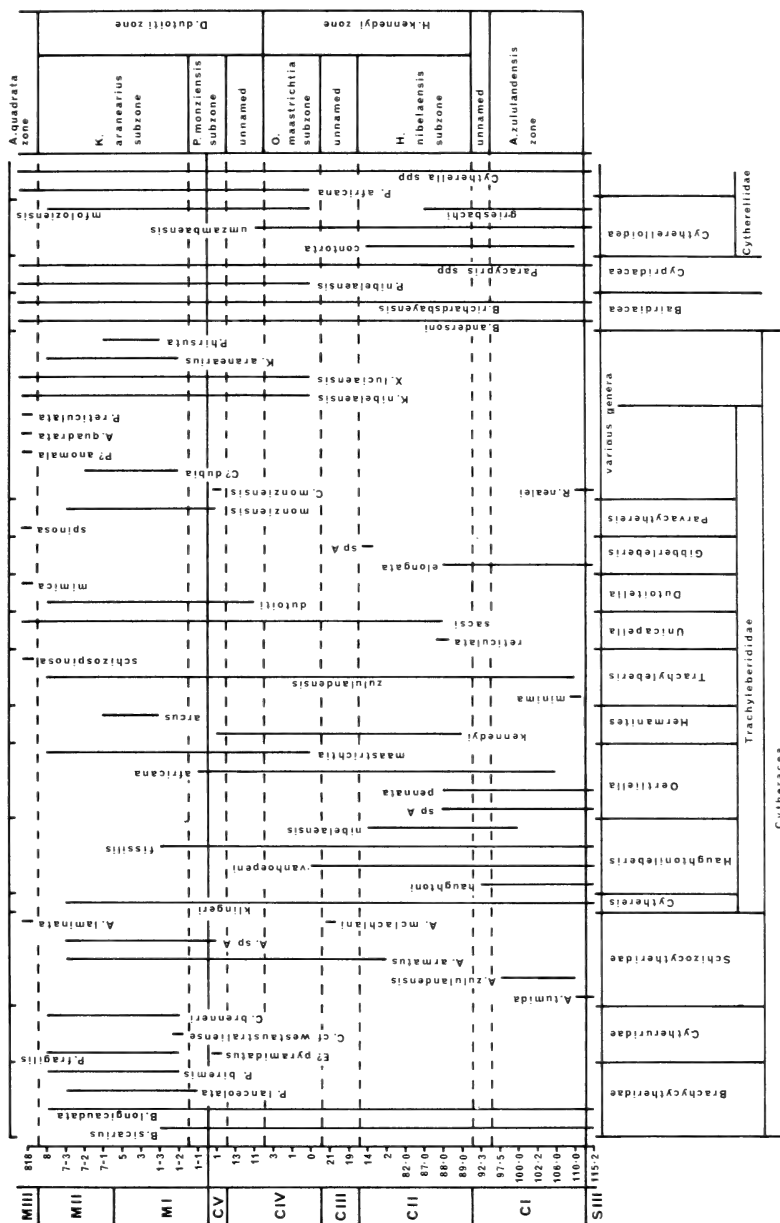


Fig. 78. Temporal distribution of ostracods, arranged by higher taxa, in Campanian–Maastrichtian strata of Zululand (BH–9, and Monzi, Mfelozi and Nibela outcrops) and Agulhas Bank. See Figure 77 for explanation of left and right-hand columns.

TABLE 16
Extant cytheracean species in Campanian-Maastrichtian of Zululand
(BH-9, and Monzi, Mfolozi and Nibela), Agulhas Bank, and Igoda.

	no. cytheracean spp	total ostracod spp	% cytheracean spp
Maastrichtian III	9	15	60
Maastrichtian II	19	29	66
Maastrichtian I	23	32	72
Campanian V	17	24	71
Campanian IV	14	22	64
Campanian III	11	17	65
Campanian II	16	24	67
Campanian I	16	24	67
Igoda	12	17	71

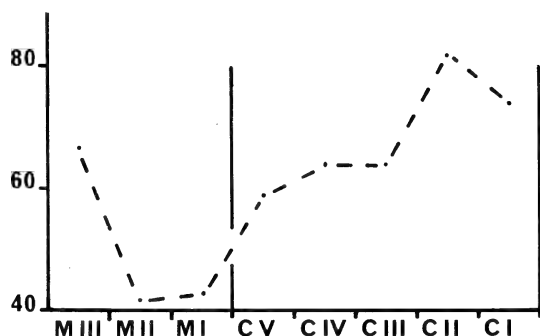


Fig. 79. Number of extant species of Trachyleberididae as a percentage of total number of cytheracean species in Campanian I-Maastrichtian III strata of south-east Africa. Data from Zululand and Agulhas Bank.

cytheracean element) are considered: 63 per cent in the Campanian and 44 per cent in the Maastrichtian. The only other diverse cytheracean families are the Brachycytheridae and Schizocytheridae (<20%) in the Campanian, which are joined by the Cytheruridae (~12%) in the Maastrichtian. However, of these, only the Schizocytheridae (21% Campanian) and Cytheruridae (25% Maastrichtian) show modest levels of evolutionary activity (expressed in terms of number of species appearing).

Whatley & Stephens (1976) made a literature survey of the worldwide Mesozoic development of the Cytheracea, and it is interesting to find that several of their conclusions are corroborated by our work in south-east Africa. At the specific level, they found that whilst the total number of new cytheracean species was higher in the Maastrichtian (375 spp compared to 360 in the Senonian, their fig. 2), expressed as a percentage of total species (their table 2), there was a decline in evolutionary activity across the Senonian-Maastrichtian boundary (76% to 65%). We have data only for the upper part of the Senonian

TABLE 17

Data on cytheracean ostracods by family in Campanian-Maastrichtian of south-east Africa.

a. Number of species appearing per stage by family (evolutionary activity of families):
Data from Zululand (BH-9, and Monzi, Mfolozi and Nibela outcrops)

	Campanian		Maastrichtian		total	
Brachycytheridae . . .	0	0	1	6%	1	3%
Cytheruridae . . .	1	5%	4	25%	5	14%
Schizocytheridae . . .	4	21%	1	6%	5	14%
Trachyleberididae . . .	12	63%	7	44%	19	54%
Cytherideidae . . .	1	5%	0	0	1	3%
Xestoleberididae . . .	1	5%	0	0	1	3%
Cytherettidae . . .	0	0	1	6%	1	3%
Bythocytheridae . . .	0	0	1	6%	1	3%
Indet.	0	0	1	6%	1	3%
	19		16		35	

b. Number of extant species per stage subdivision by family (diversity of families).
Data from Zululand and Agulhas Bank

	Camp. I	Camp. II	Camp. III	Camp. IV	Camp. V	Maas. I	Maas. II	Maas. III
Brachycytheridae . . .	2 13%	2 13%	2 18%	2 13%	2 11%	3 13%	2 11%	0 0
Cytheruridae . . .	0 0	0 0	0 0	0 0	1 6%	3 13%	2 11%	0 0
Schizocytheridae . . .	2 13%	1 6%	2 18%	1 7%	2 12%	2 9%	2 11%	1 11%
Trachyleberididae . . .	12 74%	13 82%	7 64%	9 64%	10 59%	10 43%	8 42%	6 67%
Cytherideidae . . .	0 0	0 0	0 0	1 7%	1 6%	1 4%	1 5%	1 11%
Xestoleberididae . . .	0 0	0 0	0 0	1 7%	1 6%	1 4%	1 5%	1 11%
Cytherettidae . . .	0 0	0 0	0 0	0 0	0 0	1 4%	1 5%	0 0
Bythocytheridae . . .	0 0	0 0	0 0	0 0	0 0	1 4%	1 5%	0 0
Indet.	0 0	0 0	0 0	0 0	0 0	1 4%	1 5%	0 0
	16	16	11	14	17	23	19	9

c. Total cytheraceans: Zululand and Agulhas Bank

	Campanian	Maastrichtian
Total number of species . . .	30	29
New species appearing . . .	19 63%	14 48%
Total number of genera . . .	17	23
New genera appearing . . .	1 6%	4 17%

but these suggest a similar decrease: 63 per cent (Campanian) to 48 per cent (Maastrichtian) (Table 17c). Whatley & Stephens (1976) also found that at the family level, the Trachyleberididae exhibited the highest worldwide level of cytheracean evolutionary activity during the Senonian-Maastrichtian, but detected a decrease in this activity across the Senonian-Maastrichtian boundary (~300 spp to ~250 spp, their fig. 1), which is precisely what our data show across this boundary (63% to 44%) (Fig. 79, Table 17a). The high level of cytheracean evolutionary activity, with a decrease across the Campanian-Maastrichtian boundary, and the dominance of the trachyleberids in this activity are, therefore, local manifestations of worldwide phenomena.

Other trends relating to evolution at the generic level have been noted in the taxonomic section, and suffice to summarize here by reiterating that the two most diverse genera are *Haughtonileberis* and *Oertliella* with four species each. *Haughtonileberis* is at its most diverse in Campanian I–II when all four species are extant, and, although this is the period when it reaches its greatest numerical importance in the Campanian–Maastrichtian strata, it is in reality at the latter stages of a numerical decline that commenced in the Santonian II. *Oertliella*, on the other hand, reaches its local acme much later (Campanian IV to Maastrichtian I).

Phylogeny: species distribution (extinctions)

From a commercial point of view, microfaunal data are of limited use when presented in conventional phylogenetic tables that emphasize appearances (e.g. Fig. 77). Because exploration boreholes mainly produce chippings which are liable to contaminate downhole sections, the only satisfactory way of plotting species distribution is to identify their 'tops' (extinction points, first downhole appearances). Whilst having limited scientific value, such charts are of considerable practical application, and Figure 80 shows an exploration range chart for the Campanian–Maastrichtian ostracods of south-east Africa based on their 'tops'. The ammonite stage subdivisions and the proposed ostracod zonal scheme are included.

Of the 45 species that 'appear' in the downhole sequence (i.e. locally become extinct), 26 of these do so in the Maastrichtian I and II, although the position of 11 of these cannot at present be located precisely without further sampling across the Maastrichtian II–III boundary. The ostracod zonal scheme proposed herein does not provide a more sensitive time base in this part of the stratigraphic column, and clearly further subdivision is desirable.

COMPARISON WITH OTHER GONDWANIDE LOCALITIES

Ostracods of Campanian–Maastrichtian age have been described from various Gondwanide localities in the southern hemisphere and these have been plotted on a palaeogeographical reconstruction of Gondwanaland at 65 m.y. (late Maastrichtian) (Fig. 81). Several previous workers have made comparisons of the Upper Cretaceous ostracod assemblages between the various regions of Gondwanaland (e.g. Bertels 1977; Krömmelbein 1972; Dingle 1969; Bate & Bayliss 1969; Bate 1972; Neale 1975) but all were hampered by lack of sufficient detail from south-east Africa which lay in a central position between the South Atlantic and Indian Ocean areas.

Because there are few, if any, species in common between south-east Africa and the other areas on Figure 81, comparisons of faunal similarity have to be made at the generic level. This may have serious drawbacks, not the least being taxonomic problems and the comparison of unequal statistical detail, but for a general commentary it proves useful. The percentage similarity between Campanian and Maastrichtian ostracod populations of south-east Africa (Zululand

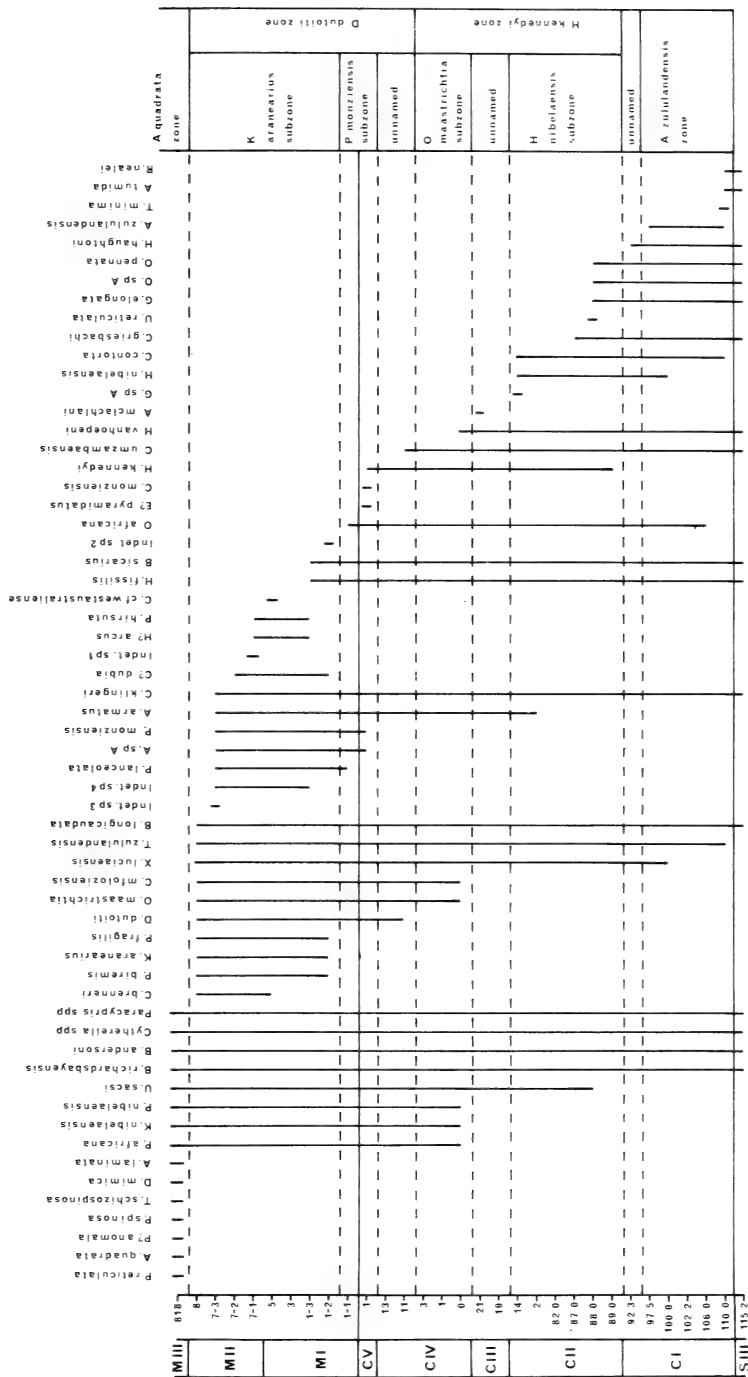


Fig. 80. Borehole exploration range chart for Campanian-Maastrichtian ostracods in Zululand (BII-9, and Monzi, Mfolozi and Nibela outcrops) and Agulhas Bank. See Figure 77 for explanation of left and right-hand columns.

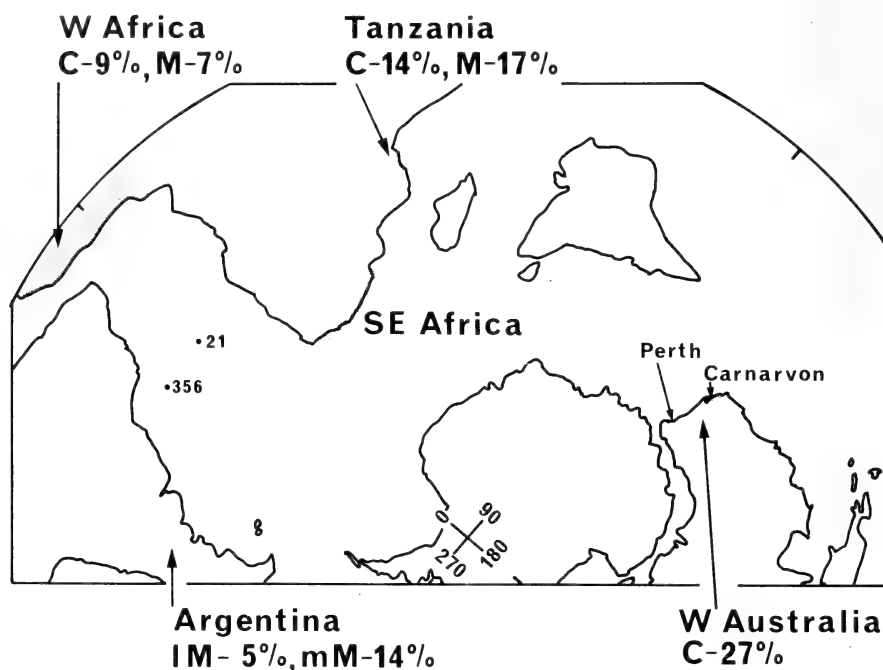


Fig. 81. Similarity at the generic level between Campanian and Maastrichtian ostracod faunas of south-east Africa (BH-9, and Monzi, Mfolozi and Nibela outcrops, Zululand) and other Gondwanide localities. Reconstruction for 65 m.y. after Firstbrook *et al.* (undated). Ostracod population data after various authors cited in the text. Abbreviations: C = Campanian, M = Maastrichtian, IM = lower Maastrichtian, mM = middle Maastrichtian.

and Sample 818) and rocks of similar ages elsewhere at generic level is shown in Figure 81. We shall briefly review these areas.

Western Australia

Campanian-Maastrichtian sediments are represented in the Carnarvon Basin of Western Australia by the Mirig Marl, Korojon Calcarenite, and Toolonga Calcilutite. Bate (1972) described the Campanian fauna of the area but gave no data on the Maastrichtian assemblages. Several of the species that Bate recorded in the Campanian were also recorded by Neale (1975) in the Santonian Gingin Chalk of the Perth Basin farther south. There is a 30 per cent inheritance of species across the Santonian-Campanian boundary in the Carnarvon Basin, with 24 per cent and 38 per cent similarity at the specific and generic levels, respectively. Table 18 shows the genera grouped into families present in the Carnarvon Basin Campanian (averaged for three samples described by Bate (1975)). Although no species are common with south-east Africa, the two areas show a relatively high (27%) generic similarity.

TABLE 18

Genera recorded in the Campanian of Carnarvon Basin, Western Australia.
% total fauna, mean of 3 samples recorded by Bate (1972).

Cytherellidae	. . .	+ <i>Cytherella</i> , + <i>Cytherelloidea</i> and + <i>Platella</i>	. . .	21%
Bairdiacea	. . .	+ <i>Bairdoppilata</i> and + <i>Bythocypris</i>	. . .	9%
Cypridacea	. . .	+ <i>Paracypris</i> and + <i>Pontocyprilla</i>	. . .	4%
Cytherideidae	. . .	+ <i>Krithe</i>	. . .	<1%
		<i>Eurotundracythere</i>	. . .	5%
Cytheruridae	. . .	+ <i>Cytheropteron</i>	. . .	10%
		<i>Oculocytheropteron</i>	. . .	<1%
		<i>Cytherura</i>	. . .	<1%
		<i>Paracytheridea</i>	. . .	<1%
		+ <i>Pedicythere</i>	. . .	<1%
Bythocytheridae	. . .	<i>Bythoceratina</i>	. . .	<1%
		<i>Cytheralisson</i>	. . .	2%
		<i>Monoceratina</i>	. . .	1%
Progonocytheridae	. . .	<i>Tickalaracythere</i>	. . .	4%
Schizocytheridae	. . .	+ <i>Apateloschizocythere</i>	. . .	12%
Pectocytheridae	. . .	<i>Premunseyella</i>	. . .	2%
Trachyleberididae	. . .	<i>Costa</i>	. . .	1%
		+ <i>Hermanites</i>	. . .	3%
		<i>Karsteneis</i>	. . .	7%
		<i>Toolongella</i>	. . .	6%
		<i>Anebocythereis</i>	. . .	2%
		+ <i>Curfsina</i>	. . .	2%
		<i>Limburgina</i>	. . .	1%
		+ <i>Oertliella</i>	. . .	4%
		+ <i>Trachyleberis</i>	. . .	1%
		<i>Orthonotocythere</i>	. . .	<1%
		<i>Hystricocythere</i>	. . .	<1%
		Genus B	. . .	1%

Similarity with south-east Africa (+):

32 genera Australia, 24 genera SE Afr., 56 total, 15 common = 27%

In addition to the cosmopolitan genera such as *Cytherella*, *Cytherelloidea*, *Bairdoppilata*, *Trachyleberis*, and *Cytheropteron*, notable similarities are *Pedicythere*, *Pariceratina* (Santonian of Perth Basin), *Apateloschizocythere*, and *Curfsina*. In addition, three species found in Western Australia, *Hermanites saggita* (Santonian–Campanian), *Oertliella exquisita* (Campanian), and *Bythocypris chapmani* (Santonian), have very close relatives in south-east Africa: *Hermanites kennedyi* (Campanian), *Oertliella maastrichtia* (Campanian–Maastrichtian), and *Bythocypris richardsbayensis* (Santonian–Maastrichtian). As Neale (1975) has pointed out, the subfamily Pennyellidae is confined to the South African–Australian–West Pacific areas, albeit at various stratigraphic levels, in the Upper Cretaceous.

Notable differences between south-east Africa and Western Australia are lack of the genera *Brachycythere* and *Haughtonileberis* in Australia, and the fact that *Majungaella/Tickalaracythere* and *Rostrocysteridea*, which are common in the Lower Cretaceous of south-east Africa, have not yet been recorded from the Upper Cretaceous of this area, whereas they do occur in the Santonian–

Campanian of Western Australia. Overall, seventeen species (numerically 53% of the Australian fauna) belong to genera not recorded from south-east Africa.

As can be seen from Figure 81, the Campanian of south-east Africa at the level of generic similarity is faunally closer to Western Australia than it is to any of the other areas of Gondwanaland.

East Africa

Ramsay (1968) and Bate (*in* Bate & Bayliss 1969) have described Campanian–Maastrichtian ostracods from Tanzania (Table 19a). Judging by the small number of specimens recorded, it would seem that the faunas have been only partially examined, and because of this, comparisons with other areas must be tentative.

The late Campanian assemblage of the Runyu inlier area shows a 14 per cent similarity at the generic level with south-east Africa, but all Bate's positive identifications were in the cosmopolitan types. His Genus B bears some resemblance to *Agulhasina*, but his sketch (Bate & Bayliss 1969, pl. 7 figs 11, 14) is not sufficient for a positive comparison. However, the Maastrichtian, with a 17 per cent generic similarity with south-east Africa, has a more varied fauna with the notable presence of *Dutoitella mimica*. Other points of similarity between the two areas are the presence in the late Turonian of Tanzania of *Brachycythere* aff. *B. sapucariensis* which Bate & Bayliss (1969) compared to *B. longicaudata* (Santonian–Maastrichtian, south-east Africa), and the similarity of three other Tanzanian Turonian species to younger south-east African counterparts: *Curfsina turonica* to *Parvacocythereis monziensis*; *Cythereis luzangaiensis* to *C. klingerii*; and the general similarity of the genus *Akrogmocythere* to *Gibberleberis*.

West Africa

Apostolescu (1961, 1963) and Reyment (1960) have documented the ostracods from various parts of west Africa (Gambia to Nigeria), and Table 19b lists the genera and species recorded by Apostolescu in his two reviews. We have no numerical population data, but the assemblages are characterized by numerous species of *Brachycythere*, *Buntonia*, *Ovocysteridea*, *Cophinia*, and *Nigeria*. Similarity, at the generic level, with south-east Africa is low (Campanian 9%, Maastrichtian 7%) and the only point of correlation between the two areas recorded so far is the relative diversity and local abundance of *Brachycythere*. *Ovocysteridea* may be represented in south-east Africa by *Pondoina*, and one species of *Veenia* (in the Santonian at Umzamba) is the only relative of *Nigeria*. Bate & Bayliss (1969: 164) have also remarked that the only point of reference between east and west Africa in the Upper Cretaceous is the presence of *Brachycythere*, though it should be noted that they also recorded *Ovocysteridea*.

Dingle (1969) concluded, after a preliminary examination of the south-east African Santonian faunas, that there is very little similarity between this area and west Africa. This conclusion is substantiated by the present, more extensive studies.

TABLE 19
Campanian-Maastrichtian ostracod genera from east and west Africa.

a. genera recorded in Tanzania (after Ramsay 1968; Bate & Bayliss 1969)

<i>Campanian</i>		<i>Maastrichtian</i>
	<i>Pterygocythereis</i>	*
	+ <i>Trachyleberis</i>	*
	+Genus C (<i>Dutoitella</i>)	*
	+ <i>Cythereis</i>	*
	+ <i>Phacorhabdotus</i>	*
*	+ <i>Krithe</i>	*
*	Genus B	
*	+ <i>Bairdoppilata</i>	*
*	+ <i>Cytherella</i>	
*	+ <i>Cytherelloidea</i>	

Similarity with south-east Africa (+):

Campanian: 5 genera E. Afr., 24 genera SE Afr., 29 total, 4 common = 14%

Maastrichtian: 7 genera E. Afr., 29 genera SE Afr., 36 total, 6 common = 17%

b. genera recorded in west Africa (after Apostolescu 1961, 1968)
(number of species in parenthesis)

<i>Campanian</i>		<i>Maastrichtian</i>
*(1)	+ <i>Brachycythere</i>	*(3)
*(3)	<i>Ovocytheridea</i>	
*(6)	<i>Buntonia</i>	*(4)
*(10)	+ <i>Cythereis</i>	*(2)
*(3)	<i>Cophinia</i>	*(1)
*(1)	<i>Nanocythere</i>	*(1)
	<i>Dactylia</i>	*(1)
	<i>Protobasslerites</i>	*(1)
	<i>Soudanella</i>	*(1)
	<i>Isobuntonia</i>	*(1)
	<i>Anticythereis</i>	*(1)
*(1)	' <i>Clithrocytheridea</i> '	
*(3)	<i>Veenia</i> (<i>Nigeria</i>)	*(5)
*(2)	+ <i>Cytherella</i>	*(2)
*(1)	<i>Sphaeroleberis</i>	*(1)

Similarity with south-east Africa (+):

Campanian: 10 genera W. Afr., 24 genera SE Afr., 34 total, 3 common = 9%

Maastrichtian: 13 genera W. Afr., 29 genera SE Afr., 42 total, 3 common = 7%

South America

The only detailed documentation from the western South Atlantic margins has been from Argentina, where Bertels (1974, 1975, 1977) has described the Lower and Middle Maastrichtian ostracods of the Jagüel Formation and its equivalents (the Campanian is represented by a non-marine facies). Two distinct faunas are evident: a very shallow marine Lower Maastrichtian fauna at the base, and an overlying Middle Maastrichtian, deeper water (?mid-shelf) assemblage (Table 20). Neither shows any strong similarity with south-east Africa, but the deeper water fauna has greater affinities (as would be expected): Lower

TABLE 20
Genera recorded in Maastrichtian of Argentina.
Data after Bertels (1974, 1975).

a. Lower Maastrichtian (Lower Jagüel Formation):

	+ <i>Cytherella</i>	6%	
	<i>Jonesia</i> ?	8%	
	<i>Cytherura</i>	8%	
	<i>Paracytheridea</i>	1%	
Trachyleberididae	<i>Alatacythere</i>	8%	} 77%
	+ <i>Trachyleberis</i>	17%	
	<i>Platacythereis</i> ?	27%	
	<i>Wichmannella</i>	25%	

Similarity with south-east Africa (+):

8 genera Argentina, 29 genera SE Africa, total 37, 2 common = 5%

b. Middle Maastrichtian (Upper Jagüel Formation):

	+ <i>Cytherella</i>	4%	
	+ <i>Bythocypris</i> ?	1%	
	+ <i>Paracypris</i>	4%	
Trachyleberididae	<i>Togoina</i>	1%	} 48%
	+ <i>Trachyleberis</i>	5%	
	<i>Actinocythereis</i>	1%	
	<i>Acanthocythereis</i>	1%	
	+ <i>Cythereis</i> ?	17%	
	<i>Henryhowella</i>	2%	
	<i>Protocosta</i>	5%	
	<i>Veenia</i> (Nigeria)	15%	
	<i>Wichmannella</i>	1%	} 21%
Hemicytheridae	<i>Bradleya</i> ?	4%	
	<i>Anticythereis</i>	17%	
Pectocytheridae	<i>Munseyella</i>	1%	
Progonocytheridae	<i>Mosaeleberis</i> ?	3%	} 6%
	<i>Tumidoleberis</i>	1%	
	<i>Sphaeroleberis</i> ?	2%	
Cytheruridae	+ <i>Cytheropteron</i>	1%	} 12%
	<i>Hemicytherura</i>	1%	
	<i>Cytheromorpha</i> ?	10%	
Schizocytheridae	+ <i>Amphicytherura</i> ?	1%	

Similarity with south-east Africa (+):

22 genera Argentina, 29 genera SE Afr., total 51, 7 common = 14%.

Maastrichtian 5 per cent and Middle Maastrichtian 14 per cent. It should be noted, however, that even this low level of similarity may be misleadingly high because it is based largely on the cosmopolitan types, *Cytherella*, *Paracypris* and *Cythereis*. Even here uncertainty is introduced by Bertel's use of '*Cythereis*' as a sack term (1975: 100): 'true *Cythereis* forms . . . do not occur in the known South American fauna.' Of the Argentinian trachyleberids (which numerically make up 48% of the population), only *Trachyleberis* occurs in south-east Africa. The similarity between Argentinian and south-east African uppermost Cretaceous ostracod faunas is, therefore, even lower than the 14 per cent suggested by Figure 81. This is in strong contrast to the lower and middle Cretaceous

faunas, where several species are common to the two areas (e.g. Musacchio 1979). Conversely, there is 14 per cent similarity at the generic level between the Maastrichtian faunas of Argentina and west Africa. Although this is the same as the Argentinian and south-east African connection, it does in reality represent a much stronger link because it occurs in characteristic trachyleberid genera such as *Togoina*, *Anticythereis*, and *Nigeria*. Significantly, the latter is numerically and specifically the most diverse and important single genus in both areas.

A similarity in deep-water faunas between south-east Africa and South America is indicated, however, by the presence of the closely related genera *Unicapella* and *Paleoabyssocythere*, and *Dutoitella* and *Atlanticythere*. Benson (1977) recorded the South American types from the Rio Grande Rise (DSDP sites 356 and 21) in the western part of the ocean basin, which at the time of deposition lay relatively close to the mid-Atlantic ridge. The South African types were deposited in water shallower than the 1 000 m suggested by Benson (1977), but whether *Unicapella* and *Dutoitella* were restricted to the continental margins is not known. If they were, then communication could have been via the Rio Grande Rise–Walvis Ridge archipelago. Conversely, they could have evolved separately from common early or mid Cretaceous ancestors.

ACKNOWLEDGEMENTS

It is a pleasure to thank Dr H. C. Klinger of the South African Museum for guidance during sample collecting in Zululand, for providing the sediment samples from Igoda and Needs Camp, and for valuable discussions on the stratigraphy of south-east Africa. I thank Dr R. Benson of the Smithsonian Institution for permission to publish sketches of some of his unpublished ostracods, and the Director of the South African Museum for the loan of Chapman's types from Needs Camp. The Management of SOEKOR kindly made available samples from the JC-1 borehole. Permission to collect samples from Umzamba was kindly granted by the Secretary to the Minister of Agriculture, Forestry, and Fisheries in the Transkei Government. Mr G. Lowcock and Dr D. Crawford of the University of Cape Town SEM unit are thanked for their assistance with photography. A University of Cape Town staff research grant is gratefully acknowledged for fieldwork and SEM expenses. The Editorial Board of the University of Cape Town provided a generous grant towards part of the publication costs for this work.

REFERENCES

- ALEXANDER, C. I. 1929. Ostracoda of the Cretaceous of North Texas. *Bull. Univ. Texas Bur. Econ. Geol.* **2907**: 1–137.
- ALEXANDER, C. I. 1933. Shell structure of the ostracode genus *Cytheropteron* and fossil species from the Cretaceous of Texas. *J. Paleont.* **7**: 181–214.
- APOSTOLESKU, V. 1961. Contribution a l'étude paléontologique (Ostracodes) et stratigraphique des bassins crétacés et tertiaires de l'Afrique occidentale. *Revue Inst. fr. Petrole* **16**: 779–867.

- APOSTOLESCU, V. 1963. Essai de zonation par les ostracodes dans le crétacé du bassin du Sénégal. *Revue Inst. fr. Petrole* **18**: 1675–1694.
- BAIRD, W. 1845. Arrangement of British Entomostraca, with a list of species, particularly noticing those which have as yet been discovered within the bounds of the Club. *Hist. Berwicksh. Nat. Club* **2**: 145–148.
- BAIRD, W. 1850. *The natural history of the British Entomostraca*: 1–364, London: Ray Society.
- BATE, R. H. 1972. Upper Cretaceous Ostracoda from the Carnarvon Basin, Western Australia. *Spec. Pap. Palaeont.* **10**: 1–85.
- BATE, R. H. & BAYLISS, D. D. 1969. An outline account of the Cretaceous and Tertiary foraminifera and of the Cretaceous ostracods of Tanzania. *Proceedings 3rd African Micropaleontological Colloquium* **1968**: 113–164, Cairo: National Information and Documentation Centre.
- BATE, R. H. & ROBINSON, E. eds. 1978. *A stratigraphical index of British Ostracoda*. Liverpool: Seel House Press.
- BENSON, R. H. 1971. A new Cenozoic deep-sea genus, *Abyssocythere* (Crustacea: Ostracoda: Trachyleberididae), with descriptions of five new species. *Smithson. Contrib. Paleobiol.* **7**: 1–25.
- BENSON, R. H. 1977. The Cenozoic ostracode faunas of the São Paulo Plateau and the Rio Grande Rise (DSDP Leg 39, Sites 356 and 357). *Initial Reports of the Deep Sea Drilling Project* **39**: 869–883. Washington: United States Government Printing Office.
- BERTELS, A. 1973. Ostracodes of the type locality of the Lower Tertiary (lower Danian) Rocanian Stage and Roca Formation of Argentina. *Micropaleontology* **19**: 308–340.
- BERTELS, A. 1974. Upper Cretaceous (lower Maastrichtian?) ostracodes from Argentina. *Micropaleontology* **20**: 385–397.
- BERTELS, A. 1975. Upper Cretaceous (middle Maastrichtian) ostracodes of Argentina. *Micropaleontology* **21**: 97–130.
- BERTELS, A. 1977. Cretaceous ostracoda—South Atlantic. In: SWAIN, F. M. ed. *Stratigraphic micropaleontology of Atlantic Basin and Borderlands*: 271–304. Amsterdam: Elsevier.
- BOSQUET, J. 1854. Monographie des crustacés fossiles du terrain Crétacé du Duché Limbourg. *Mémoires de la Commission pour la description de la Carte géologique de la Neerlande* **2**: 53–126.
- BRADY, G. S. 1880. Report on ostracoda dredged by H.M.S. 'Challenger' during the years 1873–76. *Rep. scient. Results Voy. Challenger (Zool.)* **1**(3): 1–184.
- BRADY, G. S. 1898. On new or imperfectly-known species of ostracoda, chiefly from New Zealand. *Trans. zool. Soc. Lond.* **14**: 429–452.
- BRADY, G. S., CROSSKEY, H. W. & ROBERTSON, D. 1874. *A monograph of the Post-Tertiary Entomostraca of Scotland including species from England and Ireland*. London: Palaeontographical Society.
- BRENNER, P. & OERTLI, H. J. 1976. Lower Cretaceous ostracodes (Valanginian to Hauterivian) from the Sundays River Formation, Algoa Basin, South Africa. *Bull. Cent. Rech. Pau* **10**: 471–533.
- BUTLER, E. A. & JONES, D. E. 1957. Cretaceous ostracoda of Prothro and Rayburn salt domes Bienville Parish, Louisiana. *Bull. geol. Surv. La.* **32**: 1–65.
- CHAPMAN, F. 1898. On ostracoda from the 'Cambridge Greensand'. *Ann. Mag. nat. Hist.* **3**: 331–346.
- CHAPMAN, F. 1904. Foraminifera and ostracoda from the Cretaceous of East Pondoland, South Africa. *Ann. S. Afr. Mus.* **4**: 221–237.
- CHAPMAN, F. 1916. Foraminifera and Ostracoda from the Upper Cretaceous of Need's Camp, Buffalo River, Cape Province. *Ann. S. Afr. Mus.* **12**: 107–118.
- CHAPMAN, F. 1923. On some foraminifera and ostracoda from the Cretaceous of the Umzamba River, Pondoland. *Trans. geol. Soc. S. Afr.* **26**: 107–118.
- CORYELL, H. N. & FIELDS, S. 1937. A Gatun ostracode fauna from Cativa, Panama. *Am. Mus. Novit.* **956**: 1–18.
- CORYELL, H. N., SAMPLE, C. H. & JENNINGS, P. H. 1935. *Bairdoppilata*, a new genus of ostracoda, with two new species. *Am. Mus. Novit.* **777**: 1–5.
- DAMOTTE, R. 1974. Un nouveau genre d'ostracode de l'Albien du Bassin de Paris: *Matronella* n.g. Importance des empreintes musculaires dans les attributions génériques chez les Trachyleberidinae. *Paleontographica* **146**: 181–189.

- DEROO, G. 1966. Cytheracea (Ostracodes) du Maastrichtian de Maastricht (Pays-Bas) et des régions voisines; résultats stratigraphiques et paléontologiques de leur étude. *Meded. geol. Sticht. S(C)* 2: 1–197.
- DINGLE, R. V. 1969. Upper Senonian ostracods from the coast of Pondoland, South Africa. *Trans. R. Soc. S. Afr.* 38: 347–385.
- DINGLE, R. V. 1971. Some Cretaceous ostracodal assemblages from the Agulhas Bank (South African continental margin). *Trans. R. Soc. S. Afr.* 39: 393–418.
- DINGLE, R. V. 1973. Post-Palaeozoic stratigraphy of the eastern Agulhas Bank, South African continental margin. *Mar. Geol.* 15: 1–23.
- DINGLE, R. V. 1976. Palaeogene ostracods from the continental shelf off Natal, South Africa. *Trans. R. Soc. S. Afr.* 42: 35–79.
- DINGLE, R. V. 1978. South Africa. In: MOULLADE, M. & NAIRN, A. E. M. eds. *The Phanerozoic Geology of the World II, The Mesozoic A*: 401–434. Amsterdam: Elsevier.
- DINGLE, R. V. 1980. Marine Santonian and Campanian ostracods from a borehole at Richards Bay, Zululand. *Ann. S. Afr. Mus.* 82: 1–70.
- DUCASSE, O. & GREKOFF, N. 1976. Quelques ostracodes de l'éocène inférieur du sud-ouest de l'océan Indien: Site 246, Croisière 25, 'Glomar Challenger', Deep Sea Drilling Project. *Revue Micropaléont.* 19: 134–152.
- DU TOIT, S. R. 1976. *Mesozoic geology of the Agulhas Bank, South Africa*. Unpublished Ph.D. thesis, University of Cape Town.
- DU TOIT, S. R. & LEITH, M. J. 1974. The J(c)–1 borehole on the continental shelf near Stanger, Natal. *Trans. geol. Soc. S. Afr.* 77: 247–252.
- EAGAR, S. H. 1965. Ostracoda of the London Clay (Ypresian) in the London Basin; I. Reading District. *Revue Micropaléont.* 8: 15–32.
- FIRSTBROOK, P. L., FUNNELL, B. M., HURLEY, A. M. & SMITH, A. G. (n.d.). *Paleoceanic reconstructions 160–OMA*. Washington: National Science Foundation.
- GROSDIDIER, E. 1979. Principaux ostracodes marins de l'intervalle Aptien-Turonien du Gabon (Afrique occidentale). *Bull. Cent. Rech. Expl. Prod. Elf-Aquitaine* 3: 1–35.
- GRÜNDEL, J. 1973. Zur Entwicklung der Trachyleberididae (ostracoda) in der Unterkreide und in der tieferen Oberkreide. Teil I: Taxonomie. *Z. Geol. Wiss. Berlin* 1, 11: 1463–1474.
- GRÜNDEL, J. 1974. Zur Entwicklung der Trachyleberididae (ostracoda) in der Unterkreide und in der tieferen Oberkreide. Teil II: Phylogenie. *Z. Geol. Wiss. Berlin* 2, 1: 61–71.
- GRÜNDEL, J. & KOZUR, H. 1971. Zur Taxonomie der Bythocytheridae und Tricorninidae (Podocopida, Ostracoda). *Monatsber. dt. Akad. Wiss. Berlin* 13: 907–937.
- HERRIG, E. 1965. Zwei neue *Idiocythere*-Arten aus dem Campan, Insel Rügen (Ostsee). *Geologie* 14: 1224–1235.
- HILL, B. L. 1954. Reclassification of winged *Cythereis* and winged *Brachycythere*. *J. Paleont.* 28: 804–826.
- HINTE, J. E. VAN. 1976. A Cretaceous time scale. *Bull. Am. Ass. Petrol. Geol.* 60: 269–287.
- HOLDEN, J. C. 1964. Upper Cretaceous ostracods from California. *Palaeontology* 7: 393–429.
- HOWE, H. V. & CHAMBERS, J. 1935. Louisiana Jackson Eocene ostracoda. *Bull. geol. Surv. La* 5: 1–65.
- HOWE, H. V. & LAURENCICH, L. 1958. *Introduction to the study of Cretaceous Ostracoda*. Baton Rouge: Louisiana State University Press.
- JONES, T. R. 1849. *A monograph of the Entomostraca of the Cretaceous Formations of England*. London: Palaeontological Society.
- JONES, T. R. 1884. Notes on the Foraminifera and Ostracoda from the deep boring at Richmond. *Q. Jl geol. Soc. Lond.* 40: 766–777.
- JONES, T. R. & HINDE, G. J. 1890. *A supplementary monograph of the Cretaceous Entomostraca of England and Ireland*. London: Palaeontographical Society.
- KENNEDY, W. J. & KLINGER, H. C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, stratigraphy. *Bull. Br. Mus. nat. Hist. (Geol.)* 25: 263–315.
- KLINGER, H. C., KAUFFMAN, E. G. & KENNEDY, W. J. 1980. Upper Cretaceous ammonites and inoceramids from the offshore Alphonse Group of South Africa. *Ann. S. Afr. Mus.* 82: 293–320.
- KLINGER, H. C. & KENNEDY, W. J. 1977. Upper Cretaceous ammonites from a borehole near Richards Bay, South Africa. *Ann. S. Afr. Mus.* 72: 69–107.

- KLINGER, H. C. & KENNEDY, W. J. 1980. The Umzamba Formation at its type section Umzamba Estuary (Pondoland, Transkei), the ammonite content and palaeogeographical distribution. *Ann. S. Afr. Mus.* **81**: 207–222.
- KLINGER, H. C. & LOCK, B. E. 1978. Upper Cretaceous sediments from the Igoda River Mouth, East London, South Africa. *Ann. S. Afr. Mus.* **77**: 71–83.
- KRÖMMELBEIN, K. 1964. Ostracoden aus der marinen 'Küsten-Kreide' Brasiliens. 1: *Brachycythere (Brachycythere) sapucariensis* n. sp. aus dem Turonium. *Senckenberg. Leth.* **45**: 489–495.
- KRÖMMELBEIN, K. 1972. Remarks on marine Cretaceous ostracodes of Gondwanic distribution. *Proc. 5th African Colloquium on Micropalaeontology 1972*: 539–551, Madrid: Revista Espanola de Micropalaeontologia.
- LATREILLE, P. A. 1806. *Genera Crustaceorum et Insectorum* **1**: 1–303. Paris.
- LUBIMOVA, P. S. 1955. Ostracoda of the Middle Mesozoic formations of the central Volga area and the Obshehego Sirta. In: LUBIMOVA, P. S. & CHABAROVA, T. H. eds. *Ostracoda of the Mesozoic sediments of the Volga-Urals region. Trans. All-Union Petrol. Sci. Res. Geol. Explor. Inst. (V.N.I.G.R.I.) (N.S.)* **84**: 1–189. (In Russian.)
- MAKRIDES, M. 1979. *Foraminifera of the Upper Cretaceous Mzamba Formation, Transkei, Southern Africa*. Unpublished M.Sc. Thesis, University of Witwatersrand.
- MANDELSTAM, M. I. 1960. Arthropods. In: ORLOV, Y. A. ed. *Elements of Palaeontology*. **8**: 1–515. Moscow: Geological and subsurface prospecting: Scientific and Technical Edition. (In Russian.)
- MAUD, R. & ORR, W. 1975. Aspects of post-Karoo geology in the Richards Bay area. *Trans. geol. Soc. S. Afr.* **78**: 101–109.
- MCGOWRAN, B. & MOORE, A. C. 1971. A reptilian tooth and Upper Cretaceous microfossils from the Lower Quarry at Needs Camp, South Africa. *Trans. geol. Soc. S. Afr.* **74**: 103–105.
- MCKENZIE, K. G. 1967. Recent ostracoda from Port Phillip Bay, Victoria. *Proc. R. Soc. Vict.* **80**: 61–106.
- MCLACHLAN, I. R. & McMILLAN, I. K. 1979. Microfaunal biostratigraphy, chronostratigraphy and history of Mesozoic and Cenozoic deposits on the coastal margin of South Africa. *Spec. Publs geol. Soc. S. Afr.* **6**: 161–181.
- MOORE, R. C. ed. 1961. *Treatise on Invertebrate Paleontology. Part Q, Arthropoda* **3**. Lawrence: University of Kansas Press.
- MORKHOVEN, F. P. C. M. VAN. 1962. *Post-Palaeozoic Ostracoda. Their Morphology, Taxonomy, and Economic Use. 1. General*. Amsterdam: Elsevier.
- MORKHOVEN, F. P. C. M. VAN. 1963. *Post-Palaeozoic Ostracoda. Their morphology, taxonomy, and economic use. 2. Generic descriptions*. Amsterdam: Elsevier.
- MUELLER, O. F. 1785. *Entomostraca seu insecta testacea, quae in aquis daniae et norvegiae reperit, descripsit et iconibus illustravit*. Lipsiae et Havniae.
- MÜLLER, G. W. 1894. Die Ostracoden des Golfes von Neapel und der angrenzenden Meeresabschnitte. *Fauna Flora Golf. Neapel* **31**: 1–404.
- MUSACCHIO, E. A. 1979. Datos paleobiogeograficos de algunas asociaciones de foraminiferos, ostracodos y carofitas del Jurásico medio y el Cretácico inferior de Argentina. *Ameghiniana* **16**: 247–271.
- NEALE, J. W. 1975. The ostracod fauna from the Santonian Chalk (Upper Cretaceous) of Gingin, Western Australia. *Spec. Pap. Palaeont.* **16**: 1–81.
- NEUFVILLE, E. M. H. 1979. Upper Cretaceous-Paleogene marine ostracods from the Sergipe-Alagoas Basin, north-eastern Brazil. *Bull. geol. Instn Univ. Uppsala* **8**: 135–162.
- OERTLI, H. J. 1963. *Mesozoic ostracod faunas of France*, Leiden: Brill.
- POKORNY, V. 1964. *Oertliella* and *Spinicythereis*, new ostracod genera from the Upper Cretaceous. *Vest. ustred. Ust. geol.* **39**: 283–284.
- POKORNY, V. 1967. The genus *Curfsina* (Ostracoda, Crustacea) from the Upper Cretaceous of Bohemia, Czechoslovakia. *Acta Univ. Carol. Geologica* **4**: 345–364.
- POSTUMA, J. A. 1971. *Manual of Planktonic Foraminifera*. Amsterdam: Elsevier.
- PURI, H. S. 1954. Contribution to the study of the Miocene of the Florida Panhandle. Part III (Ostracoda). *Bull. geol. Surv. Fla* **3**: 217–309.
- PURI, H. S. 1955. *Hermanites*, a new name for *Hermania* Puri 1954. *J. Paleont.* **29**: 558.
- REUSS, A. E. 1846. *Die Versteinerungen der böhmischen Kreide Formation* **2**: 59–148. Stuttgart; Schweizerbart.

- RAMSAY, W. V. 1968. A new morphological aspect of the ostracode genus *Cytherelloidea* Alexander. *Micropaleontology* **14**: 348–356.
- REYMENT, R. A. 1960. Studies on Nigerian Upper Cretaceous and Lower Tertiary Ostracoda. Part 1: Senonian and Maastrichtian Ostracoda. *Stockh. Contr. Geol.* **8**: 1–238.
- ROSENFELD, A. & BEIN, A. 1978. A preliminary note on recent ostracodes from shelf to rise sediments off north-west Africa. *Meteor ForschErgebn.* **29**: 14–20.
- SARS, G. O. 1866. Oversigt af Norges marine ostracoden. *Forh. VidenskSelsk. Krist.* **7**: 1–130.
- SARS, G. O. 1888. Nye Bidrag til Kundskaben om Midlehavets Invertebrat fauna 4. Ostracoda Mediterranea. *Arch. Math. Naturv.* **12**: 173–324.
- SARS, G. O. 1922–1928. *An account of the Crustacea of Norway* **9**. Ostracoda, Parts 1–16: 1–277. Bergen: Bergen Museum.
- SIESSER, W. G. & MILES, G. A. 1979. Calcareous nannofossils and planktic foraminifers in Tertiary limestones, Natal and eastern Cape, South Africa. *Ann. S. Afr. Mus.* **79**: 139–158.
- SIMON, W. & BARTENSTEIN, H. 1962. *Leitfossilien der mikropaläontologie*. Berlin-Nikolassee: Gebrüder Bornträger.
- SOEKOR, 1976. *Structure of the Mesozoic succession of the Agulhas Bank*. Johannesburg: Technical Department, Southern Oil Exploration Corporation.
- SYLVESTER-BRADLEY, P. C. 1948. The ostracode genus *Cythereis*. *J. Paleont.* **22**: 792–797.
- SYLVESTER-BRADLEY, P. C. & BENSON, R. H. 1971. Terminology for surface features in ornate ostracods. *Lethaia* **4**: 249–286.
- SWAIN, F. M. 1946. Upper Jurassic Ostracoda from the Cotton Valley Group in northern Louisiana; the genus *Hutsonia*. *J. Paleont.* **20**: 119–129.
- TRIEBEL, E. 1941. Zur Morphologie und Oekologie des Fossilen Ostracoden. Mit Beschreibung einiger neuer Gattungen und Arten. *Senckenberg. Leth.* **23**: 294–400.
- TRIEBEL, E. 1952. Ostracoden der Gattung *Cytheretta* aus dem Tertiär des Mainzer Beckens. *Notizbl. hess. Landesamt. Bodenforsch. Wiesbaden* **6**: 15–30.
- WHATLEY, R. C. & STEPHENS, J. M. 1976. The Mesozoic explosion of the Cytheracea. *Abl. Verh. naturw. Ver. Hamburg* **18/19**: 63–76.

6. **SYSTEMATIC** papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- (a) The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- (b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

R. V. DINGLE

THE CAMPANIAN AND MAASTRICHTIAN
OSTRACODA OF SOUTH-EAST AFRICA

VOLUME 85 PART 2

JANUARY 1982

ISSN 0303-2515

507 68

ANNALS

OF THE SOUTH AFRICAN
MUSEUM

CAPE TOWN



INSTRUCTIONS TO AUTHORS

1. **MATERIAL** should be original and not published elsewhere, in whole or in part.

2. **LAYOUT** should be as follows:

- (a) *Centred masthead to consist of*
Title: informative but concise, without abbreviations and not including the names of new genera or species
Author's(s') name(s)
Address(es) of author(s) (institution where work was carried out)
Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract* of not more than 200 words, intelligible to the reader without reference to the text
- (c) *Table of contents* giving hierarchy of headings and subheadings
- (d) *Introduction*
- (e) *Subject-matter* of the paper, divided into sections to correspond with those given in table of contents
- (f) *Summary*, if paper is lengthy
- (g) *Acknowledgements*
- (h) *References*
- (i) *Abbreviations*, where these are numerous

3. **MANUSCRIPT**, to be submitted in triplicate, should be typewritten and neat, double spaced with 2.5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

4. **ILLUSTRATIONS** should be reducible to a size not exceeding 12×18 cm (19 cm including legend); the reduction or enlargement required should be indicated; originals larger than 35×47 cm should not be submitted; photographs should be rectangular in shape and final size. A metric scale should appear with all illustrations, otherwise magnification or reduction should be given in the legend; if the latter, then the final reduction or enlargement should be taken into consideration.

All illustrations, whether line drawings or photographs, should be termed figures (plates are not printed; half-tones will appear in their proper place in the text) and numbered in a single series. Items of composite figures should be designated by capital letters; lettering of figures is not set in type and should be in lower-case letters.

The number of the figure should be lightly marked in pencil on the back of each illustration.

5. **REFERENCES** cited in text and synonymies should all be included in the list at the end of the paper, using the Harvard System (*ibid.*, *idem*, *loc. cit.*, *op. cit.* are not acceptable):

(a) Author's name and year of publication given in text, e.g.:

- 'Smith (1969) describes ...'
'Smith (1969: 36, fig. 16) describes ...'
'As described (Smith 1969a, 1969b; Jones 1971)'
'As described (Haughton & Broom 1927) ...'
'As described (Haughton *et al.* 1927) ...'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
et al. in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969a, 1969b) and not Smith (1969, 1969a).

For books give title in italics, edition, volume number, place of publication, publisher.

For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

Examples (note capitalization and punctuation)

- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **85** Band
January **1982** Januarie
Part **2** Deel



MICROMAMMALS AS
PALAEOENVIRONMENTAL INDICATORS AND
AN INTERPRETATION OF THE LATE
QUATERNARY IN THE SOUTHERN CAPE
PROVINCE, SOUTH AFRICA

By

D. M. AVERY

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33, 45(1)

EDITOR/REDAKTRISE

Ione Rudner

Copyright enquiries to the South African Museum

Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 86813 028 1

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

MICROMAMMALS AS PALAEOENVIRONMENTAL INDICATORS AND AN INTERPRETATION OF THE LATE QUATERNARY IN THE SOUTHERN CAPE PROVINCE, SOUTH AFRICA

By

D. M. AVERY

South African Museum, Cape Town

(With 33 figures and 50 tables)

[MS accepted 3 March 1981]

ABSTRACT

Micromammalian remains recovered from several archaeological sites in the southern Cape Province are examined in an attempt to ascertain the potential of such material for providing evidence of palaeoenvironmental change. Analyses of the composition and structure of the small mammal communities represented and of the mean size of individuals in populations of different ages and locations are checked against existing evidence from other lines of research. The micromammalian evidence, which here covers approximately the last 80 000 years, is shown to be both reliable and informative on a fine scale. The possibility of using the micromammalian evidence to correlate undated or insecurely dated archaeological sequences is discussed. Consideration is also given to the application of the data to archaeological interpretation and general theories concerning human technological development.

CONTENTS

	PAGE
Introduction	184
The southern Cape Province	186
The sites	189
Archaeological sites	189
Modern sites	200
The material	207
Agency of accumulation	207
Methods of collection	209
Identification	210
The nature of excavated samples	213
The nature of micromammalian evidence	217
Methods	228
Computation of minimum numbers	228
Multivariate statistical analysis of primary data	229
Processes for interpreting analyses	234
Mensuration and calculation of indices	235
The modern data	238
Ecological distribution	238
The basis for interpretation	243
Interpretation of comparative samples	246
Micromammalian evidence for palaeoenvironmental change	253
Evidence from community composition	253
Evidence from mean size variation	277
Evidence from species diversity	307

	PAGE
Palaeoenvironmental reconstruction based on micromammalian evidence	314
Boomplaas A	314
Byneskranskop 1	318
Die Kelders 1 Middle Stone Age samples	320
Coastal samples	322
Holocene and modern samples	323
Upper Pleistocene and modern samples	324
Existing evidence for Late Quaternary environments	326
Marine evidence	327
Terrestrial evidence	330
Correlation of micromammalian and existing evidence	335
General framework	336
Southern African evidence	338
Macromammalian evidence	339
Micromammalian evidence for site correlation	347
Prehistory and environmental change	351
General considerations	352
The southern Cape Province	356
Conclusions	362
Summary	364
Acknowledgements	365
References	365

INTRODUCTION

Micromammalian remains were first used as indicators of past environmental conditions in South Africa by De Graaff (1960). His preliminary investigation of the Lower to Middle Pleistocene rodent faunas from the Krugersdorp (Transvaal) australopithecine-bearing deposits included a short section on the climatic variations between the different sites, referring in particular to the degree of aridity or humidity. Cartmill (1967) also interpreted the micromammalian evidence from these sites in terms of annual rainfall, providing support for the hypothesis that *Paranthropus* was adapted to moister conditions than was *Australopithecus*. Brain (1974) discussed the use of microfaunal remains from archaeological sites as habitat indicators. He postulated (Brain 1974: 58), for instance, that the presence of *Eremitalpa granti* in the Mirabib deposits in the Namib Desert could be used to indicate the advance of dune fields across the Kuiseb River. This is because *E. granti* has been shown to be restricted to soft sand, whereas at present the Mirabib Hills are surrounded by a gravel plain for 20 km in all directions. In fact, Brain & Brain (1977) subsequently concluded that, in the absence of *E. granti*, the dune fields were blocked by the river. They have further suggested (Brain & Brain 1977: 293) that fluctuations in the proportions of gerbils and geckos reflect changes in the amount of rainfall and, consequently, of vegetation. Following on this line, the present study comprises a comprehensive examination of micromammalian remains from a number of southern Cape archaeological sites containing Upper Pleistocene and Holocene deposits. The purpose is to examine the nature and

potential of this material and to establish the extent to which the evidence obtainable from the material supports or refines current knowledge of climatic and vegetational fluctuations during approximately the last 80 000 years.

The principal interest in the present work, as in that of Brain (1974; Brain & Brain 1977), is to contribute detailed information concerning the conditions under which people lived in prehistoric times. This is a basic aspect of prehistoric studies since it has become increasingly clear that human cultural adaptation and development must be viewed in the context of the contemporary natural, that is physical and biological, environment of the people concerned. In pursuance of the general aim, the collection for study of micromammalian remains from archaeological sites has two main advantages. These sites comprise one or more discrete units containing durable remains of human activities in the past. Where several such units accumulate in a stratified sequence they may well represent a considerable period of time. Micromammalian remains, although apparently not collected by humans, frequently become admixed with the archaeological material, either in the same or in intervening units. They, therefore, provide evidence of conditions pertaining over the same general period of time as that covered by the archaeological samples, but with the important quality of being independent of the archaeological evidence. For archaeology, a potential application of the detailed micromammalian evidence for environmental change is that of assessing the possible effect of such change on cultural development. This is particularly the case where units can be shown by absolute dating to represent relatively short periods of time since the resolution will then be correspondingly tight. Another potentially useful aspect of the study is the provision of a means of dating sites relatively. Where absolute dates are lacking, it may be possible to use detailed evidence of environmental change to provide relative dates.

The southern Cape was chosen as the region of study partly because, being here defined as that area bounded by the sea and the Cape Folded Mountains, it forms a convenient natural unit. Primarily, however, it was chosen because the number of samples of micromammalian material available from this natural unit provided maximum potential for investigation. Good sequences of samples have been collected from three sites in the area. These are Boomplaas A in the Cango valley, and Byneskranskop 1 and Die Kelders 1 near and on the Walker Bay coast. Other samples come from Klasies River Mouth 1A and from Nelson Bay Cave, both on the south coast. The available samples allowed conditions during the Upper Pleistocene (Last Glacial) and Holocene (Present Interglacial) to be examined. The Boomplaas A data are unique in that they provide evidence of glacial maximum and full interglacial conditions and thus probably illustrate the range of variation in response by micromammalian communities which is to be expected for this area. Modern micromammalian material was examined both for control purposes and in order to see whether change had occurred during approximately the last 2 000 years since the end of the subfossil record available from the archaeological sites.

The question of the agency responsible for accumulating the micromammalian remains in caves and any possible idiosyncrasies of that agent which may bias composition of the samples, was investigated in some detail. The nature of the evidence forthcoming from the micromammalian remains was also examined. This concerns factors pertaining to micromammals as well as factors connected with samples recovered from archaeological or palaeontological sites. All these considerations will have a potential bearing on the interpretations which it is possible to make from the material. Any inherent strengths or weaknesses must be clearly recognized. Another integral part of the study involved establishing as precisely as possible the environmental significance of individual species as well as the possible reasons for fluctuations in population size or community structure. In this exercise it was necessary to generalize to a certain extent because data concerning specific factors governing distribution and reproduction are not available for most of the species.

Data from other disciplines which provide evidence for climatic and vegetational change were examined in order to provide a context for the study and also to check the validity of the interpretations made from the micromammalian evidence. The general framework is known and has been confirmed from a number of different lines of investigation. At the local level, however, much remains to be done. The micromammalian evidence provides detail at this level and suggests that differential change may be detectable on quite a fine scale within one region.

Two main lines of investigation were pursued in attempting to interpret the material. The major of these involved examining variations in the structure of the small mammal community as a whole. Changes in the dominant species, as well as fluctuations in the proportions of numerically less important species, suggest changing environmental conditions which it is possible to interpret within the limits of the evidence. In most cases changes in proportions of plant life-forms will be reflected directly whereas evidence for climatic change will be indirect. Changes in species diversity appear also to give some general indication of changing conditions. At the population level, differences in the mean size of individuals in different populations of selected species indicate physical response to varying climatic conditions of which they are thus evidence. Although interpretation is currently hampered by lack of comparative modern data, the extent to which this study is yet able to augment present knowledge of environmental change during the Upper Pleistocene and Holocene confirms the potential of these investigations.

THE SOUTHERN CAPE PROVINCE

The southern Cape Province is here defined as that part of the Cape Province which lies south of 33°S (Fig. 1). At this latitude the east-west branch of the Cape Folded Mountains bounds a coastal plain between Cape Hangklip in the west and Cape St Francis in the east. The region under discussion has

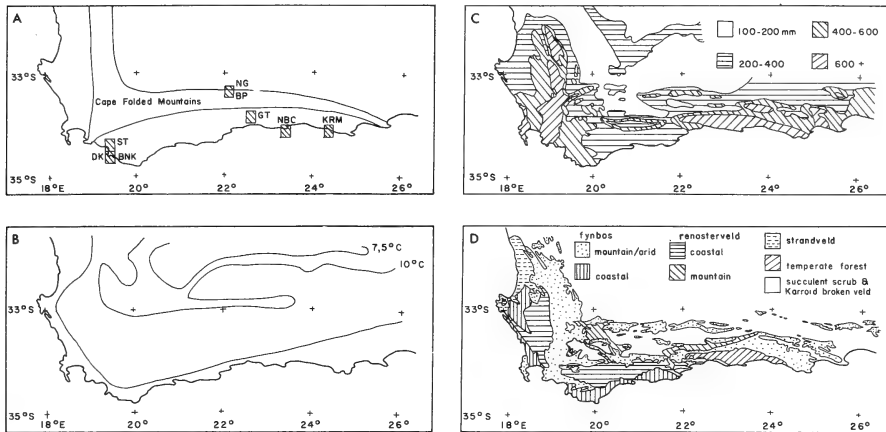


Fig. 1. The southern Cape Province. A. Location of described sites. (Position of Cape Folded Mountains based on Hendey 1974.) B. Mean July temperature (based on Schulze 1965). C. Rainfall (after Van Zinderen Bakker 1976). D. Vegetation (after Kruger 1977).

been ascribed to parts of geomorphologic provinces 14, 15 and 16 by King (1963), and to part of region 11 by Wellington (1955). The east-west branch of the Cape Folded Mountains comprises two principal subparallel ranges, the northern Swartberg and southern Langeberg Mountains. These are extremely rugged with deep river-cut gorges crossing them at intervals. Boomplaas A is one of a series of caves, including the famous Congo Caves, which is formed along a fault zone in the foothills of the Swartberg Mountains (Roussouw *et al.* 1964: 87). Between the two mountain ranges lies the Little Karoo which, although flatter, is still hilly and rocky. The coastal plain tends to be undulating with some low hills into one of which Byneskranskop 1 and 2 are cut. The caves that are situated on the present coastline, namely, Die Kelders 1, Nelson Bay Cave and Klasies River Mouth 1A, were incised by the sea during past transgressions.

The western part of the region has a Mediterranean climate with winter rainfall (Schulze 1965). Further east the rainfall is year-round, gradually giving way to a summer rainfall régime in the south-eastern Cape. Annual rainfall varies greatly, from as much as 3 000 mm in some mountain valleys to as little as 250 mm in the Little Karoo and rain-shadow areas such as the Breede River valley. Extremes of temperature are greatest inland, in the mountains and Little Karoo, where there is very marked variation in temperature at different times both of the day and the year. Such a continental régime is in contrast to that of the coastal region, where temperatures are considerably less variable and generally mild, with frost being almost unknown.

The natural vegetation of the southern Cape principally comprises fynbos (Fig. 1). This is basically restricted to the winter rainfall area where the mean

annual rainfall is at least 250 mm. In general, fynbos is characterized by a lack of single species dominance and/or conspicuous presence of Restionaceae, and physiognomically by restioid, ericoid and proteoid elements (Taylor 1978: 174). Three major subdivisions have, however, been recognized (Kruger 1977; Taylor 1978). Mountain fynbos tends to have several layers, particularly on the lower slopes which are characterized by proteoid shrubs, usually 1,5 to 2,5 m in height. Arid fynbos, which occurs as a narrow belt along the inland lower slopes of the Cape Folded Mountains (Taylor 1978: 199), tends to be more open than mountain fynbos, with a simpler structure and a preponderance of ericoid forms. The coastal fynbos includes many more grasses than the mountain fynbos, with the south-coast variant tending to comprise a lower ericoid layer and a taller proteoid layer.

Strandveld is another type of vegetation that occurs in the coastal regions of the southern Cape. Elements of fynbos and forest play a part in the succession of this type. From pioneer grasses the succession proceeds to a climax of coastal scrub, the highest development of which is represented by small forest patches occurring near Stanford (Taylor 1961). Low scrub or sward occurs in moist depressions near the coast. Coastal renosterveld, dominated by the renosterbos (*Elytropappus rhinocerotis*), separates the vegetation of the coastal plain from that of the mountains. Its rich flora includes many species of grasses (Taylor 1978: 216). Mountain renosterveld occupies a similar transitional position between the mountain fynbos and the Karoo vegetation. It occurs at medium altitudes and contains narrow-leaved dwarf shrubs (Werger 1978: 284). Unlike the coastal renosterveld which has fynbos affinities, the mountain variety contains a considerable Karoo element. Between the mountain ranges the Little Karoo bears a vegetation of shrubs and dwarf shrubs with a dominance of succulents and few grasses. Afromontane temperate forest occurs as enclaves in the southern Cape, principally near Knysna but also on suitably watered and sheltered southern slopes as far west as Table Mountain (White 1978: 507). The forest varies from being comparable to Afromontane rainforest in structure to scrubforest and thicket in less suitable conditions.

The intergradation of one type of vegetation into another illustrates the dynamic nature of the delicate equilibrium between the various types. The region of the Congo valley provides a very good example of the complexity that may exist and of the interaction of different vegetations. In this case the rich flora reflects the intermediate position of the valley between the moist Swartberg Mountains and the drier Little Karoo (Moffett & Deacon 1977: 128). Five major phytogeographic elements have been recognized in this one area and vegetation assignable to four of Acocks' (1975) veld types occurs in the valley. It is to be expected, particularly in such a complicated situation, that even minor changes in climate would alter the balance, and there is now direct evidence from botanical data and indirect evidence from the macromammalian material of such past changes.

THE SITES

The sites from which the material for this study was collected are all caves or rock shelters. Within such caves and rock shelters there is a tendency for debris to build up as a result of the use of these places as shelters by animals and humans. Over a period of time such debris may accumulate in layers to a considerable thickness. According to the picture of human occupation patterns which is emerging from archaeological study, it would appear that occupation of the caves by people was periodic (e.g. Parkington 1972, 1976; Deacon & Brooker 1976). Relative increase in the proportion of micromammalian remains in levels not connected with human occupation indicates the alternate use of the caves by owls (see below for discussion on the predator involved) and presumably other animals, particularly birds. The process of accumulation of layers of micromammalian-rich matrix can be observed in operation in caves and rock shelters today. Collections were subsequently made from such sites in an attempt to elucidate conditions prevailing at various times in the past.

ARCHAEOLOGICAL SITES

The sites are described below in alphabetical order. In each case the location of the site is given, together with the period represented by the deposits and the cultural sequence as interpreted by the archaeologists who have studied the human occupation of the site. Some indication is also given of the quality of the micromammalian samples and the horizons from which they were extracted.

Boomplaas A (BPA)

Boomplaas A (33°23'S 22°11'E) is situated in the Cango valley about 40 km north of Oudtshoorn, which lies in the Little Karoo (Figs 1–2). It is part of a fissure system in the Drupkelderkop, some 600 m above sea-level in the foothills of the Swartberg Mountains. There are approximately 5 m of deposits (Fig. 3). The time range covered by these deposits is from about 80 000 B.P. to about 1 500 B.P. (Deacon *et al.* 1976). There is a period of leaching and wash about half-way down the sequence, somewhere between $14\,200 \pm 240$ B.P. and $21\,000 \pm 420$ B.P., which probably represents a short hiatus (Deacon & Brooker 1976: 209; H. J. Deacon 1976 pers. comm.). Deacon & Brooker (1976) give a general description of the sequence, noting that contributions to the deposits were made at various times by material entering through a fissure at the back of the cave, through the front of the cave by human and other agency, and as a result of roof spalls and rock tumble. Deacon *et al.* (1976) give a more detailed description of the top third of the sequence. Figure 3 is based on the most recent description by Deacon (1979). The cultural sequence begins with Middle Stone Age (M.S.A.) at the bottom. This is succeeded at about 32 000 B.P. by an upper M.S.A. industry with long quartzite blades. This is, in turn, replaced first by an as yet undescribed industry of non-Levallois character

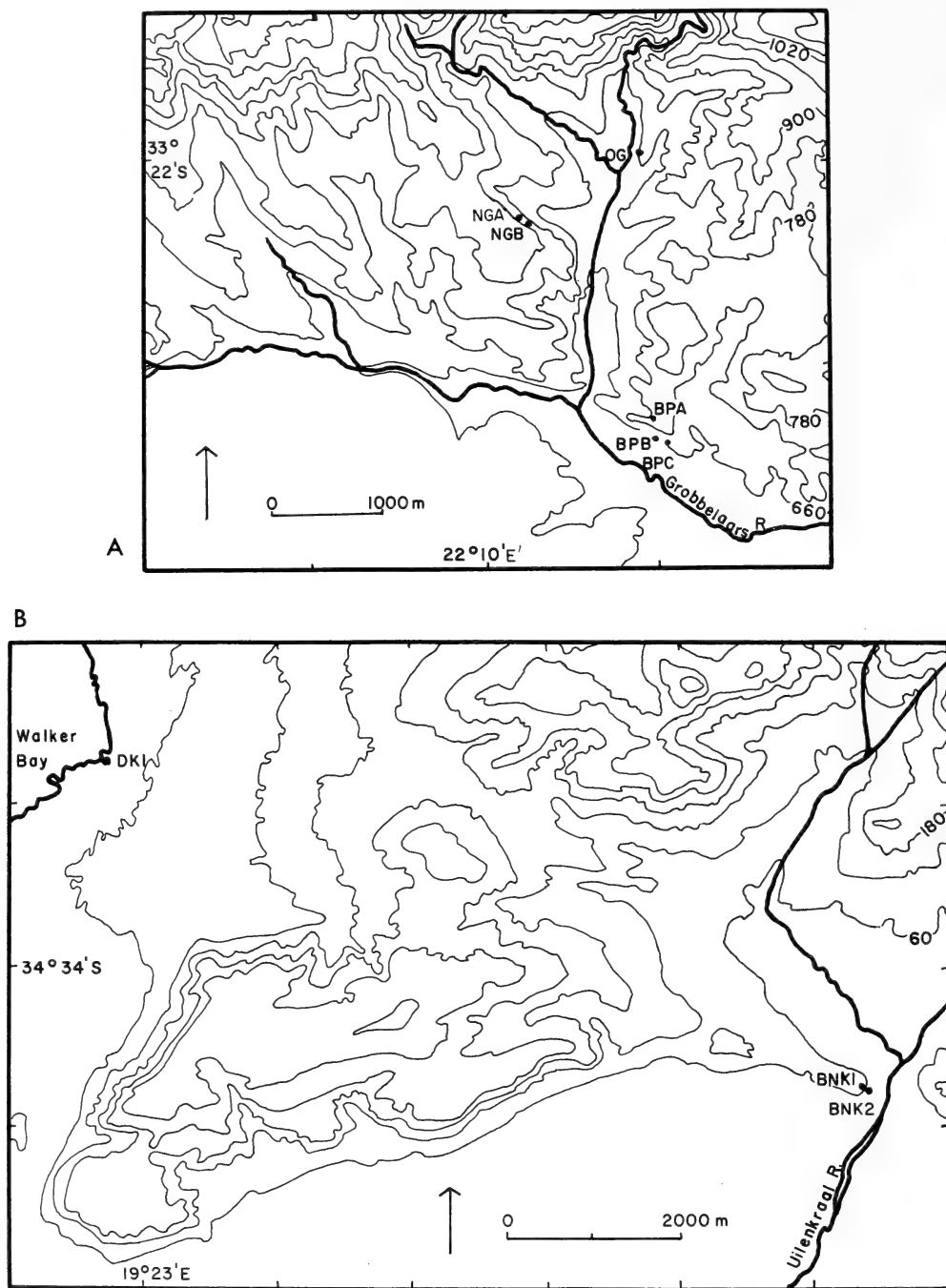


Fig. 2. Detailed location of sites. A. In the Congo valley. B. On the Walker Bay coast. (After Avery 1977.)

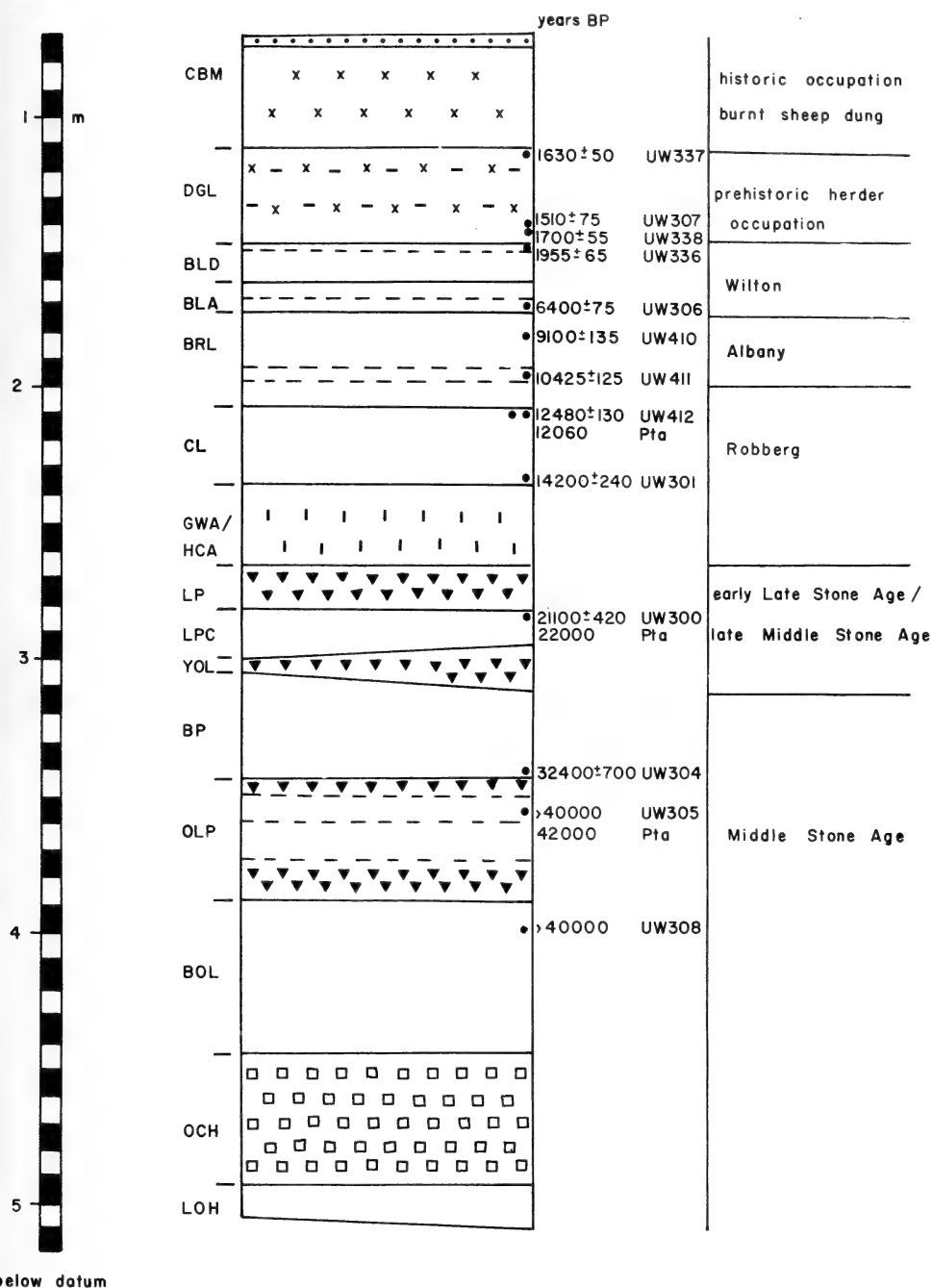


Fig. 3. Diagrammatic section of Boomplaas A with lithological units, ^{14}C determinations and cultural units (after Deacon 1979).

TABLE I
Percentage representation of species in samples from lower levels in the Boomplaas A test square P12.

	YOL	BP1	BP2	BP3	BP4	OLP	OLP1	OLP2	OLP3	BOL	BOL1	BOL2	BOL3	BOL4	BOL5	OCH	LOH
INSECTIVORA																	
<i>C. duthiae</i>	4.98	3.13	0.87	3.06	2.32	4.08	2.20	3.02	2.22	2.46	2.70	—	3.70	2.80	1.02	1.86	2.46
<i>E. edwardi</i>	0.31	0.52	0.87	—	0.17	—	0.16	0.05	0.13	0.16	—	11.11	—	—	1.02	0.19	0.82
<i>M. varius</i>	27.10	38.64	18.26	19.39	24.89	28.80	39.53	49.77	38.46	32.51	10.81	11.11	—	13.08	26.53	23.75	27.05
<i>Myosorex</i>	1.25	5.48	2.61	4.08	3.15	1.36	4.23	3.56	3.09	1.71	—	—	—	0.93	1.02	0.74	—
<i>S. varilla</i>	2.18	5.74	2.61	—	1.60	2.45	3.54	3.55	6.16	1.71	1.35	—	—	—	—	1.30	1.64
<i>C. cyanea</i>	—	—	—	1.02	2.16	1.09	1.81	1.94	1.21	0.64	1.35	—	—	—	—	1.30	1.64
<i>C. flavescens</i>	3.12	0.78	2.61	5.10	2.10	2.72	0.87	1.14	0.76	1.55	5.41	—	11.11	11.21	3.06	2.78	2.46
sub-total	38.94	54.31	27.83	32.65	36.39	40.49	52.36	56.02	52.04	40.32	21.62	22.22	14.81	28.04	32.65	31.91	36.07
CHIROPTERA																	
<i>R. clivosus</i>	—	—	—	—	0.06	—	0.08	0.07	0.16	0.16	—	—	—	—	—	0.19	0.82
<i>R. capensis</i>	—	0.26	—	—	0.06	—	0.08	0.06	0.09	0.11	—	—	—	—	—	—	—
<i>M. lesueur</i>	—	—	—	—	—	—	—	0.02	—	—	—	—	—	—	—	—	—
<i>M. tricolor</i>	0.31	0.26	—	—	0.17	—	0.16	0.15	0.18	0.27	—	—	—	—	—	0.19	—
<i>E. hottentotus</i>	—	—	—	—	0.06	—	—	—	—	—	—	—	—	—	—	—	—
<i>E. capensis</i>	—	—	—	—	—	0.27	—	0.02	0.04	0.05	—	—	—	—	—	—	—
<i>M. schreibersi</i>	—	—	—	—	0.06	0.27	—	0.03	0.02	—	—	—	—	—	—	0.19	0.82
sub-total	0.31	0.52	—	—	0.39	0.54	0.31	0.35	0.49	0.59	—	—	—	—	—	0.56	1.64
RODENTIA																	
<i>R. hottentotus</i>	5.92	3.13	13.04	10.20	6.53	5.16	3.70	3.67	2.76	3.69	9.46	11.11	7.41	9.35	11.22	9.09	4.10
<i>A. subspinosus</i>	—	1.31	0.87	1.02	0.80	1.36	0.63	0.78	0.87	1.02	1.35	—	—	—	—	0.37	0.82
<i>A. nanuquensis</i>	1.25	1.57	2.61	2.04	4.42	2.17	2.13	2.42	2.42	2.73	2.70	11.11	7.41	2.80	1.02	2.41	2.46
<i>D. incanatus</i>	0.31	—	0.87	1.02	0.74	—	0.24	0.04	0.18	0.32	—	—	—	—	—	0.37	0.82
<i>M. minutoides</i>	0.31	1.04	0.87	—	0.72	1.36	1.65	2.01	1.88	0.91	—	—	—	0.93	—	0.19	0.82
<i>P. verrucosus</i>	0.31	0.26	1.74	2.04	0.83	0.54	0.39	0.49	0.54	0.91	1.35	—	—	—	—	0.37	0.82
<i>R. penitelo</i>	0.31	0.52	—	1.02	0.80	1.09	0.71	0.75	0.63	0.96	1.35	—	—	—	1.02	1.30	0.82
<i>M. albicaudatus</i>	0.31	—	—	1.02	0.17	0.27	1.10	0.65	0.47	0.48	4.05	11.11	3.70	—	1.02	1.86	2.46
<i>T. afra</i>	—	—	—	—	0.17	—	0.16	0.06	0.02	0.04	—	—	—	—	—	—	0.82
<i>G. pabra</i>	—	—	—	—	—	—	—	0.01	0.04	0.05	—	—	—	—	—	—	0.82
<i>D. melanotis</i>	1.56	3.39	3.48	1.02	1.66	2.45	2.76	2.68	3.34	2.46	1.35	—	—	—	—	0.74	—
<i>D. mesomelas</i>	—	0.26	—	—	0.06	—	0.24	0.14	0.18	0.05	—	—	—	—	—	0.19	—
<i>Dendromus</i>	0.31	1.83	1.74	1.02	1.93	2.17	1.81	2.03	2.40	1.76	—	—	—	1.02	—	0.56	—
<i>S. krebsi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>S. campestris</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. laminitus</i>	0.62	0.52	—	1.02	0.06	0.27	0.08	0.24	0.13	0.05	2.70	—	—	—	1.02	0.37	—
<i>O. saundersae</i>	30.22	17.23	23.48	33.67	32.25	26.09	19.06	19.96	17.00	25.94	33.78	33.33	38.32	27.55	31.54	31.54	28.69
<i>O. irradians</i>	13.71	12.53	17.39	10.20	12.11	15.22	12.05	7.53	13.75	16.95	20.27	11.11	29.63	17.76	19.39	15.58	18.03
<i>O. unisulcatus</i>	—	1.04	6.09	2.04	0.22	0.54	0.31	0.04	0.43	0.37	—	—	7.41	0.93	4.08	1.86	—
<i>G. ocellatus</i>	5.30	0.52	—	—	0.33	0.27	0.31	0.13	0.43	0.43	—	—	1.87	—	—	0.74	—
sub-total	60.75	45.17	72.17	67.35	63.22	58.97	47.32	43.63	47.47	59.09	78.38	77.78	85.19	71.96	67.35	67.53	62.30
N =	321	383	115	98	1808	368	1270	10100	4464	1870	74	9	27	107	98	539	122

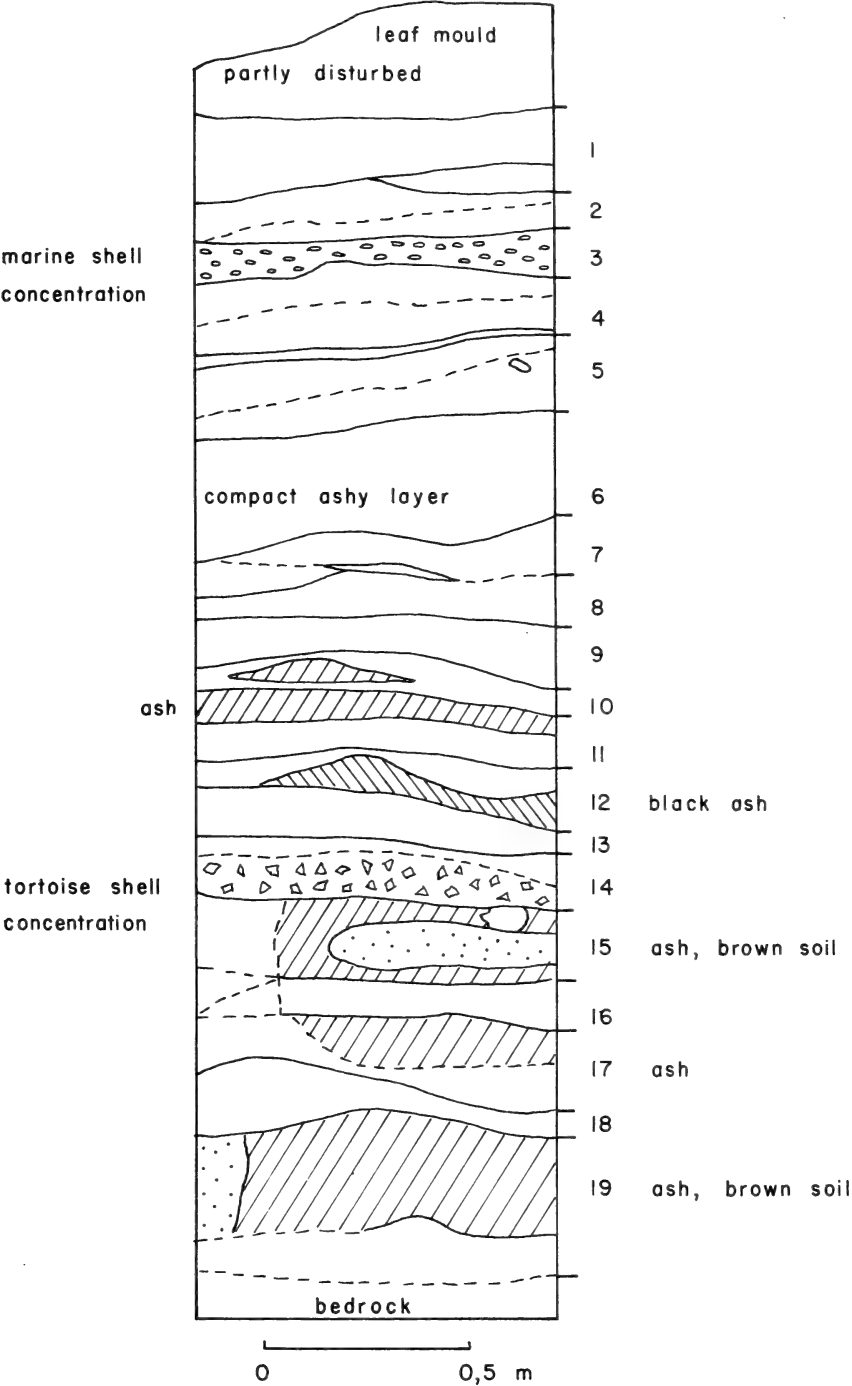


Fig. 4 Section 028/29 at Byneskranskop 1 (after Schweitzer & Wilson 1978).

TABLE 2

Percentage representation of species in samples from upper levels in main excavation at Boomplaas

	DGL1	DGL2	BLD2	BLD2A	BLD3	BLD3A	BL	BLA	BRL	B
INSECTIVORA										
<i>C. duthiae</i>	—	0,42	1,08	—	0,78	0,71	1,06	0,16	0,48	(
<i>E. edwardi</i>	1,18	1,26	1,08	0,99	0,78	0,71	1,42	0,99	2,40	
<i>M. varius</i>	7,10	8,82	4,30	3,47	6,07	4,48	3,90	6,73	5,29	
? <i>Myosorex</i>	0,59	—	—	0,50	0,47	0,47	0,35	0,16	—	
<i>S. varilla</i>	0,59	0,42	—	—	—	1,18	0,71	1,64	1,92	(
<i>C. cyanea</i>	4,14	4,20	3,23	1,98	2,18	2,36	4,61	1,64	1,92	(
<i>C. flavescens</i>	11,24	13,87	9,68	14,85	12,15	11,56	13,12	11,00	10,58	
sub-total	24,85	28,99	19,35	21,78	22,43	21,46	25,18	22,33	22,60	2
CHIROPTERA										
<i>R. clivus</i>	—	—	1,08	—	0,16	0,24	—	—	0,48	(
<i>R. capensis</i>	—	—	—	—	0,31	—	—	0,16	—	
? <i>M. lesueuri</i>	—	—	—	—	—	—	—	—	—	(
<i>M. tricolor</i>	—	—	—	—	—	—	—	0,16	—	
<i>E. hottentotus</i>	—	—	—	—	0,16	—	—	—	—	
<i>E. capensis</i>	—	—	—	—	—	—	—	—	—	
<i>M. schreibersi</i>	—	—	—	—	—	—	—	—	—	
sub-total	—	—	1,08	—	0,62	0,24	—	0,33	0,48	(
RODENTIA										
<i>C. hottentotus</i>	11,24	11,76	17,20	24,26	18,69	16,27	12,41	12,97	6,73	
<i>A. subspinosus</i>	0,59	0,84	—	—	0,16	0,47	2,13	0,66	0,48	
<i>A. namaquensis</i>	11,24	10,50	9,68	7,43	7,01	8,02	7,09	9,03	14,42	1
<i>D. incommis</i>	—	—	—	0,50	0,31	0,24	—	0,16	—	
<i>M. minutoides</i>	1,18	0,42	—	0,50	0,47	0,94	0,35	0,99	0,48	
<i>P. verreauxi</i>	1,18	—	1,08	2,48	0,62	0,47	1,06	0,82	3,37	
<i>R. pumilio</i>	2,37	2,94	—	2,48	2,34	4,01	2,48	0,99	0,96	
<i>M. albicaudatus</i>	1,18	5,04	6,45	4,95	5,76	6,60	8,51	6,40	5,77	
<i>T. afra</i>	—	—	—	—	0,16	0,47	0,71	0,49	—	
<i>G. paeba</i>	—	—	—	—	0,16	0,24	—	0,16	0,48	
<i>D. melanotis</i>	—	0,42	—	—	0,16	0,24	0,35	0,33	0,48	(
<i>D. mesomelas</i>	—	—	—	—	—	—	—	—	—	
? <i>Dendromus</i>	0,59	0,42	1,08	0,50	0,16	—	0,35	0,33	—	
<i>S. krebsi</i>	—	0,42	3,23	0,50	1,25	2,36	3,19	1,64	2,40	
<i>S. campestris</i>	1,78	1,68	1,08	0,99	1,40	1,42	1,77	0,49	0,96	
<i>O. laminatus</i>	1,18	0,84	1,08	—	0,31	0,47	0,71	0,49	0,48	
<i>O. saundersae</i>	7,10	5,88	10,75	6,93	8,10	7,55	6,74	8,21	6,25	
<i>O. irroratus</i>	34,32	28,99	26,88	25,74	27,26	26,89	25,89	31,36	32,69	2
<i>O. unisulcatus</i>	1,18	0,84	1,08	0,99	2,49	1,65	1,06	1,81	0,96	
<i>G. ocularis</i>	—	—	—	—	0,16	—	—	—	—	
sub-total	75,15	71,01	79,57	78,22	76,95	78,30	74,82	77,34	76,92	7
N =	169	238	93	202	642	424	282	609	208	

at about 24 000 B.P., and then by the Robberg industry at about 20 000 B.P. Thereafter, at the end of the Pleistocene or the beginning of the Holocene, about 11 000 B.P., the Albany industry succeeded the Robberg industry and was itself replaced by the Wilton industry by about 6 500 B.P. at the latest. Whilst it is presumable that the makers of all of these industries were hunter-gatherers, domestic stock appears to have been introduced into the site about 1 700 B.P. This phenomenon was accompanied by a significant reduction in the number of stone tools recovered (Deacon *et al.* 1978: 47).

The samples of microfauna from much of the lower half of the sequence are large even though they were available only from the test square metre (Table 1). The sample from the upper half is also good now that it has been augmented by material from the extended excavation (Tables 2–3). This latter sample comprised a considerable number of subsamples based on lithological units observed in the excavation.

BRL4	BRL5	BRL6	BRL7	CL1	CL2	CL3 BG	GWA TBF	GWA	LP GGU	LP GGL	LPM	LPC 2B
0,43 3,70 3,91 — 0,87 3,04 7,83	1,01 2,03 8,10 0,25 1,01 2,78 4,05	0,52 1,04 6,48 — 2,07 2,33 7,51	0,72 1,44 6,22 — 1,67 3,11 5,74	1,94 — 5,81 0,22 1,08 3,11 7,53	3,60 0,72 13,67 2,16 1,44 2,16 10,79	5,23 0,23 15,00 0,23 1,14 1,36 4,32	2,89 0,14 26,17 3,99 1,52 — 1,79	3,13 — 25,28 7,95 1,69 — 1,28	3,27 — 30,39 4,25 2,61 — 2,29	3,59 — 22,99 3,02 0,86 — 2,30	2,74 0,11 22,11 6,42 1,16 — 2,53	3,25 — 39,61 7,14 1,30 — 1,95
19,78	19,24	19,95	18,90	19,14	34,53	27,50	36,50	39,33	42,81	32,76	35,05	53,25
0,22 — — — 0,22 —	0,25 — — — — —	0,26 — 0,26 — 0,26 —	— 0,24 — — — —	— — — — — —	— — 0,72 — — —	— 0,45 — 0,23 — —	0,14 — — — — —	0,16 — — 0,16 — —	0,33 — — — — —	0,14 0,14 — 0,14 — —	0,21 — — 0,11 — 0,11	— — — — — —
0,43	0,25	0,78	0,24	—	0,72	0,68	0,14	0,32	0,33	0,57	0,53	—
11,96 1,09 17,61 0,22 0,22 4,35 0,87 3,48 — — 0,43 0,22 0,22 0,87 — 0,87 6,97 28,48 1,52 0,43	11,39 0,76 15,44 0,25 0,51 2,53 1,27 3,04 0,25 0,25 — — 0,25 — — — 1,01 — 25,32 1,77 0,25	14,51 — 10,88 0,26 0,26 2,59 1,81 3,37 0,26 0,26 — — 0,78 — — — 1,55 30,83 0,26 —	16,51 1,20 7,89 0,48 0,48 1,91 1,20 3,11 0,24 0,24 — — 0,24 — — — 0,48 36,60 0,24 0,24	20,43 0,22 10,75 0,43 0,22 0,43 0,86 1,94 — — — — — — — — 1,08 29,03 1,08 0,22	10,79 0,72 10,07 — — 0,72 1,44 1,44 — — — — — — — — 0,72 20,14 — 0,72	22,73 0,45 6,14 — — 0,91 1,82 1,14 — — — — — — — — 1,36 21,59 0,23 0,23	7,30 0,28 1,79 0,14 0,28 0,16 0,55 0,28 — — — — — — — — 0,14 7,02 4,27 0,14	4,25 0,24 1,61 0,08 0,32 0,16 0,32 0,24 — — — — — — — — 0,16 39,57 6,18 5,38	3,92 — 2,61 — — 0,33 0,65 — — — — — — — — — — 30,72 12,42 4,58 —	5,60 0,29 1,72 0,14 0,29 0,29 0,43 0,29 — — — — — — — — 0,14 41,38 10,20 3,59	4,00 0,21 1,79 0,11 0,53 0,53 0,84 0,42 — — — — — — — — 39,89 9,89 4,32 0,21	1,95 0,65 1,95 — 0,65 0,65 1,95 0,65 — — — — — — — — 24,68 6,49 3,90 —
79,78	80,51	79,27	80,86	80,86	64,75	71,82	63,36	60,35	56,86	66,67	64,42	46,75
460	395	386	418	465	139	440	726	1246	306	696	950	154

Byneskranskop 1 (BNK1)

Byneskranskop 1 (34°35'S 19°28'E) lies some 9,5 km south-east of Die Kelders. It is situated 60 m above sea-level in the side of a small limestone hill near the Uilenkraal River (Figs 1–2). There are approximately 3 m of deposits spanning the last 12 500 years without major breaks. The stratigraphy (Fig 4) comprises mainly dark-grey soil interspersed with ash bands and a prominent band each of shell and tortoise bones (Schweitzer & Wilson 1978). The cultural sequence is divided broadly into two industries, a 'pre-Wilton' in levels 19 to 10, and a Wilton in levels 9 upwards (Schweitzer & Wilson 1978). Further subdivisions of these major divisions into a total of five subgroups are possible but have not yet been refined. Pottery was recovered from the highest levels.

The microfaunal samples from the pre-pottery levels is adequate (Table 4); that from the pottery levels was too small to warrant examination.

TABLE 2

Percentage representation of species in samples from upper levels in main excavation at Boomplaas

	DGL1	DGL2	BLD2	BLD2A	BLD3	BLD3A	BL	BLA	BRL	BRL1	BRL2	BRL3	BRL4	BRL5	BRL6	BRL7	CL1	CL2	CL3	BG	GWA	TBF	GWA	LP	GGU	LP	GGU	LPM	LPC	2B
INSECTIVORA																														
<i>C. dufrenoyi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>E. edwardsi</i>	1.18	1.26	1.08	0.99	0.78	0.71	1.42	0.99	2.40	0.70	1.70	1.80	1.04	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44	1.44
<i>M. varius</i>	7.10	8.82	4.30	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Myosorex</i>	0.59	0.42	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>S. varilla</i>	4.14	4.20	3.23	1.98	2.18	2.36	4.61	1.64	1.92	2.33	3.04	2.78	2.33	3.11	2.58	2.16	1.36	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>C. gwyni</i>	11.24	13.87	9.68	14.85	12.15	11.56	13.12	11.00	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58	10.58
<i>C. flavescens</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sub-total	24.85	28.99	19.35	21.78	22.43	21.46	25.18	22.33	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60	22.60
CHIROPTERA																														
<i>R. elvovus</i>	—	—	1.08	—	0.16	0.24	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>R. capensis</i>	—	—	—	—	0.31	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>M. leucurus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>M. tricolor</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>E. hottentotus</i>	—	—	—	—	0.16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>E. capensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>M. schreibersi</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sub-total	—	—	1.08	—	0.62	0.24	—	0.33	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48
RODENTIA																														
<i>C. hottentotus</i>	11.24	11.76	17.20	24.26	18.69	16.27	12.41	12.97	6.71	10.44	11.96	11.39	14.51	16.51	20.43	10.79	22.73	7.30	4.25	3.92	5.60	4.00	1.94	—	—	—	—	—	—	—
<i>A. subspinosus</i>	0.59	0.84	—	—	0.16	0.47	2.13	0.66	0.44	0.21	0.99	0.76	—	1.20	0.22	0.72	0.45	0.28	0.24	—	—	—	—	—	—	—	—	—	—	—
<i>A. namaquensis</i>	11.24	10.50	9.68	7.43	7.01	8.02	7.09	9.03	14.42	10.32	17.61	15.44	10.88	7.89	10.75	10.07	6.14	1.79	1.61	2.61	1.72	1.79	1.95	—	—	—	—	—	—	—
<i>D. incertus</i>	—	—	—	—	0.50	0.31	0.24	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16	0.16
<i>M. minutoides</i>	1.18	0.42	—	—	0.50	0.47	0.34	0.35	0.99	0.48	0.23	0.25	0.26	0.48	0.43	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>P. verrucosus</i>	1.18	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>R. pumilio</i>	2.37	2.94	—	—	2.48	2.34	4.01	2.48	0.99	0.96	1.72	0.87	1.27	1.81	1.20	0.86	1.44	1.82	0.55	0.32	0.65	0.43	0.84	1.95	—	—	—	—	—	—
<i>M. albicaudatus</i>	1.18	5.04	6.45	4.95	5.76	6.60	8.51	6.40	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77	5.77
<i>T. afro</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>G. pachy</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>D. melanotis</i>	—	0.42	—	—	—	0.16	0.24	0.35	0.33	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48	0.48
<i>D. mesomelas</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>D. dendromus</i>	0.59	0.42	1.08	0.50	0.16	—	—	0.35	0.33	—	—	—	—	0.22	0.25	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>S. krebsi</i>	—	0.42	3.23	0.50	1.25	2.36	3.19	1.64	2.40	1.64	0.87	1.01	1.55	0.48	1.08	0.72	1.36	0.14	0.16	—	—	—	—	—	—	—	—	—	—	—
<i>S. campestris</i>	1.78	1.68	1.08	0.99	1.40	1.42	1.77	0.49	0.56	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. lamnatus</i>	1.18	0.84	1.08	—	0.31	0.47	0.71	0.49	0.48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. saundersi</i>	7.10	5.88	10.75	6.93	8.10	7.55	6.74	8.21	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25	6.25
<i>O. irroratus</i>	34.32	28.99	26.88	25.74	27.26	26.89	25.89	31.36	32.69	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89	25.89
<i>O. unilobatus</i>	1.18	0.84	1.08	0.99	0.16	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>G. ocellatus</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
sub-total	75.15	71.01	79.57	78.22	76.95	78.30	74.82	77.34	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91	76.91
N =	169	238	93	202	642	424	282	609	208	301	460	395	386	418	465	139	440	726	1246	306	696	950	154	—	—	—	—	—	—	—

at about 24 000 B.P., and then by the Robberg industry at about 20 000 B.P. Thereafter, at the end of the Pleistocene or the beginning of the Holocene, about 11 000 B.P., the Albany industry succeeded the Robberg industry and was itself replaced by the Wilton industry by about 6 500 B.P. at the latest. Whilst it is presumable that the makers of all of these industries were hunter-gatherers, domestic stock appears to have been introduced into the site about 1 700 B.P. This phenomenon was accompanied by a significant reduction in the number of stone tools recovered (Deacon *et al.* 1978: 47).

The samples of microfauna from much of the lower half of the sequence are large even though they were available only from the test square metre (Table 1). The sample from the upper half is also good now that it has been augmented by material from the extended excavation (Tables 2-3). This latter sample comprised a considerable number of subsamples based on lithological units observed in the excavation.

Byneskranskop 1 (BNK1)

Byneskranskop 1 (34°35'S 19°28'E) lies some 9.5 km south-east of Die Kelders. It is situated 60 m above sea-level in the side of a small limestone hill near the Uilenkraal River (Figs 1-2). There are approximately 3 m of deposits spanning the last 12 500 years without major breaks. The stratigraphy (Fig 4) comprises mainly dark-grey soil interspersed with ash bands and a prominent band each of shell and tortoise bones (Schweitzer & Wilson 1978). The cultural sequence is divided broadly into two industries, a 'pre-Wilton' in levels 19 to 10, and a Wilton in levels 9 upwards (Schweitzer & Wilson 1978). Further subdivisions of these major divisions into a total of five subgroups are possible but have not yet been refined. Pottery was recovered from the highest levels.

The microfaunal samples from the pre-pottery levels is adequate (Table 4); that from the pottery levels was too small to warrant examination.

TABLE 3

Percentage representation of species in excavation units in the main excavation at Boomplaas A.

	DGL	BLD3	BL	BLA	BRL	CL	GWA	LP	LPC
INSECTIVORA									
<i>C. duthiae</i> . . .	0,38	0,75	1,06	0,16	0,62	2,74	3,04	3,13	3,25
<i>E. edwardi</i> . . .	1,15	0,75	1,42	0,99	2,59	0,55	0,05	0,05	—
<i>M. varius</i> . . .	5,11	5,44	3,90	6,73	5,63	9,44	25,61	23,72	39,61
? <i>Myosorex</i> . . .	0,26	0,47	0,35	0,16	0,28	0,34	6,49	4,87	7,14
<i>S. varilla</i> . . .	0,26	0,47	0,71	1,64	1,24	1,30	1,62	1,28	1,30
<i>C. cyanea</i> . . .	3,83	2,25	4,61	1,64	2,48	2,33	—	—	—
<i>C. flavescens</i> . . .	13,54	11,91	13,12	11,00	7,09	5,68	1,47	2,41	1,95
sub-total . . .	24,52	22,05	25,18	22,33	19,92	23,05	38,29	35,45	53,25
CHIROPTERA									
<i>R. clivovus</i> . . .	0,13	0,19	—	—	0,28	—	0,15	0,20	—
<i>R. capensis</i> . . .	—	0,19	—	0,16	—	0,21	—	0,05	—
<i>M. lesueurii</i> . . .	—	—	—	—	—	—	—	—	—
<i>M. tricolor</i> . . .	—	—	—	0,16	0,11	0,14	0,10	0,10	—
<i>E. hottentotus</i> . . .	—	0,09	—	—	—	—	—	0,05	—
<i>E. capensis</i> . . .	—	—	—	—	0,11	—	—	0,05	—
<i>M. schreibersi</i> . . .	—	—	—	—	—	—	—	0,05	—
sub-total . . .	0,13	0,47	—	0,33	0,51	0,34	0,25	0,51	—
RODENTIA									
<i>C. hottentotus</i> . . .	16,35	17,73	12,41	12,97	11,25	19,08	5,38	4,56	1,95
<i>A. subspinosus</i> . . .	0,51	0,28	2,13	0,66	0,90	0,62	0,25	0,20	0,65
<i>A. namaquensis</i> . . .	9,32	7,41	7,09	9,03	15,48	8,48	1,67	1,90	1,95
<i>D. incomtus</i> . . .	0,26	0,28	—	0,16	0,28	0,27	0,10	0,10	—
<i>M. minutoides</i> . . .	0,38	0,66	0,35	0,99	0,39	0,21	0,30	0,36	0,65
<i>P. verreauxi</i> . . .	1,15	0,56	1,06	0,82	3,32	1,03	0,15	0,41	0,65
<i>R. pumilio</i> . . .	2,17	3,00	2,48	0,99	1,24	1,30	0,41	0,67	1,95
<i>M. albicaudatus</i> . . .	4,09	6,10	8,51	6,40	3,71	1,98	0,25	0,31	0,65
<i>T. afra</i> . . .	—	0,28	0,71	0,49	0,17	0,07	—	—	—
<i>G. paeba</i> . . .	—	0,19	—	0,16	0,17	0,07	—	—	—
<i>D. melanotis</i> . . .	0,13	0,19	0,35	0,33	0,51	0,48	0,91	1,33	1,30
<i>D. mesomelas</i> . . .	—	—	—	—	0,23	0,14	—	0,05	—
? <i>Dendromus</i> . . .	0,51	0,09	0,35	0,33	0,11	0,07	0,81	0,41	1,95
<i>S. krebsi</i> . . .	0,77	1,69	3,19	1,64	0,79	—	—	—	—
<i>S. campestris</i> . . .	1,28	1,41	1,77	0,49	0,11	—	—	—	—
<i>O. laminatus</i> . . .	0,64	0,38	0,71	0,49	0,96	0,96	0,15	0,05	—
<i>O. saundersae</i> . . .	6,77	7,88	6,74	8,21	9,85	12,93	39,40	38,99	24,68
<i>O. irrortatus</i> . . .	29,76	27,11	25,89	31,36	28,36	28,11	6,49	10,40	6,49
<i>O. unisulcatus</i> . . .	1,15	2,16	1,06	1,81	1,58	0,48	4,97	4,10	3,90
<i>G. ocularis</i> . . .	0,13	0,09	—	—	0,17	0,27	0,20	0,20	—
sub-total . . .	75,35	77,49	74,82	77,34	79,57	76,61 +	61,46	64,04	46,75
N =	783	1066	282	609	1777	1462	1972	1952	154
+ Includes Muridae indet. 0,07%.									
DGL = DGL — BLD2A									
BLD3 = BLD3 and BLD3A									
BRL = BRL — BRL6									
CL = BRL7 — CL3BG									
GWA = GWATBF and GWA									
LP = LPGGU — LPM									

Die Kelders 1 (DK1)

Die Kelders 1 (34°32'S 19°22'E) is situated on the Walker Bay coast some 5 km north-west of Gansbaai (Figs 1–2). The cave is presently 8 m above sea-level. There are more than 7 m of deposits but approximately 1 m of these represents a period of non-occupation between the Middle Stone Age and the Late Stone Age. Tankard & Schweitzer (1974, 1976) have suggested that the former occupation lasted from about 80 000 B.P. to about 35 000 B.P. There are two published dates for the M.S.A. (Schweitzer 1970: 136) which were obtained using the apatite fraction of bone; one of these seems unlikely and the other is inconclusive. The former, GX-1716, from level 3, is $11\,200 \pm 700$ B.P. which by comparison with other sites is far too young. The latter, GX-1717,

from level 5, is $31\,800 \pm \begin{smallmatrix} 5000 \\ 2900 \end{smallmatrix}$ B.P., which could fit the circumstantial dating given by Tankard (1976a: 156). There is a series of dates from the L.S.A. occupation, ranging from $2\,020 \pm 95$ B.P. (GX-1686) to $1\,456 \pm 100$ B.P. (GX-1685). Tankard & Schweitzer (1974, 1976) discuss the geology of the site and Figure 5 is based on their sections. Accumulated upon quartzite boulders and sand are six M.S.A. occupation levels interleaved with layers of sand. Near the top of the M.S.A. sequence a massive rock-fall was probably caused by an earthquake (Tankard & Schweitzer 1976: 310). Thereafter, at the height of the Last Glacial, the cave was uninhabitable, first because of standing water and then because of blockage of the entrance by a sand-dune. Only at about 2 000 B.P. was the cave re-occupied, this time by Wilton people who subsisted largely on shellfish and other marine resources.

Although adequate microfaunal samples were obtained from most of the M.S.A. levels, there is a tendency for larger numbers of individuals to have been accumulated at times when the cave was thought not to have been occupied by people (Tankard & Schweitzer 1974: 367) (see Table 5). This is similar to a tendency for rodent bones to be present only when human occupation was not intense, which was noted at Redcliff Cave in Zimbabwe by Brain (1960: 132).

Klasies River Mouth 1A (KRM1A)

Klasies River Mouth 1A (34°07'S 24°24'E) is one of series of seven caves containing archaeological material which is situated within a distance of about 2 km along the coast some 40 km west of Cape St Francis (Fig. 1). KRM1A is presently 6–8 m above sea-level (Wymer & Singer 1972: 207). According to Butzer (1978), levels 33 to 22 comprise alternating well-stratified hearth zones and light grey silty sand. Levels 21 to 10 comprise silty sands with some coarse sands, while levels 9 to 1 again comprise silty sands but with a greater abundance of artefactual debris. KRM1A contains both M.S.A. and L.S.A. levels, of which the former date from perhaps 125 000 B.P. to about 65 000 B.P. (Bada & Deems 1975), while the latter were deposited during the last 5 000 years (Klein 1976). The M.S.A. has been divided into five industrial units, M.S.A. I and II, Howieson's Poort, and M.S.A. III and IV, of which the first is the oldest. The L.S.A. has been divided into I and II with the latter being the younger.

One of the two numerically adequate micromammalian samples from this site comes from level 15 which is a Howieson's Poort level; the other comes from level 32 which is an M.S.A. II level (Table 6).

Nelson Bay Cave (NBC)

Nelson Bay Cave (34°06'S 23°22'E) is located on the west face of the Robberg peninsula just west of Plettenberg Bay at about 19–21 m above sea-level (Fig. 1). The deposits reach a depth of about 5 m and have been discussed in detail by Butzer (1973) and the section given here (Fig. 6) is based

TABLE 4

Percentage representation of species in samples from Byneskranskop 1.

	1	2	3	4	5	6	7	8
INSECTIVORA								
<i>C. asiatica</i>	2,70	—	—	3,33	1,41	1,92	3,05	2,1
<i>E. edwardi</i>	—	—	—	1,67	—	—	—	—
<i>M. varius</i>	13,51	8,70	—	10,00	17,46	20,05	19,08	18,5
<i>S. varilla</i>	4,05	—	—	1,67	5,65	7,42	9,92	7,6
<i>C. cyanea</i>	—	4,35	—	1,67	—	—	—	—
<i>C. flavescens</i>	14,86	13,04	20,00	16,67	12,58	14,01	8,40	10,9
sub-total	35,14	26,09	20,00	35,00	37,10	43,41	40,46	39,3
CHIROPTERA								
<i>R. clivosus</i>	1,35	—	—	1,67	0,26	0,55	—	—
<i>R. capensis</i>	1,35	4,35	—	3,33	0,26	—	0,76	1,0
<i>M. tricolor</i>	—	—	—	—	0,13	—	—	—
<i>E. hottentotus</i>	—	—	—	—	0,13	—	—	—
<i>E. capensis</i>	—	—	—	—	—	—	—	—
<i>M. schreibersi</i>	—	—	—	—	0,26	0,27	—	0,5
sub-total	2,70	4,35	—	5,00	1,03	0,82	0,76	1,6
RODENTIA								
<i>C. hottentotus</i>	—	—	—	—	0,64	—	0,76	—
<i>G. capensis</i>	8,11	21,74	40,00	10,00	4,62	5,22	7,63	3,2
<i>A. subspinosus</i>	—	—	—	—	0,39	0,27	—	0,5
<i>A. namaquensis</i>	—	—	—	—	—	—	—	—
<i>D. incomtus</i>	—	—	—	—	—	0,27	—	—
<i>M. minutoides</i>	1,35	—	—	—	1,41	0,55	0,76	2,1
<i>P. verreauxi</i>	4,05	—	—	3,33	3,59	2,47	3,05	2,7
<i>R. pumilio</i>	5,41	8,70	20,00	1,67	2,57	1,65	0,76	2,1
<i>M. albicaudatus</i>	5,41	4,35	—	5,00	3,98	3,30	1,53	3,2
<i>T. afra</i>	5,41	8,70	—	5,00	3,72	1,65	3,82	1,6
<i>D. melanotis</i>	1,35	—	—	—	1,80	0,82	1,53	1,6
<i>D. mesomelas</i>	—	—	—	—	0,26	0,82	0,76	0,5
? <i>Dendromus</i>	1,35	—	—	—	—	—	—	0,5
<i>S. krebsi</i>	13,51	8,70	—	11,67	20,41	19,51	19,08	23,5
<i>O. laminatus</i>	—	—	—	—	0,90	0,82	0,76	0,5
<i>O. saundersae</i>	9,46	4,35	—	11,67	12,07	12,91	12,21	9,2
<i>O. irroratus</i>	6,76	13,04	20,00	11,67	5,52	5,49	6,11	7,1
sub-total	62,16	69,57	60,00	60,00	61,87	55,77	58,78	59,0
N =	74	23	5	60	779	364	131	18

on this work. The lower half of the sequence consists mainly of iron humate-stained loams while the upper half comprises mainly shell material in a sandy loam matrix. M.S.A. material was found in the lower third of the deposits below a rubble horizon which Klein (1972a: 184; 1974a: 272) considered at one time to have been accumulated during a period of about 10 000–15 000 years when the cave was not occupied. The existence of comparable industries at Nelson Bay Cave and at Klasies River Mouth suggests, however, that the Nelson Bay Cave M.S.A. occupation might have lasted from about 120 000 B.P. to perhaps 90 000 B.P. Above the rubble horizon, the late Upper

9A	9B	10	11	12	13	14	15	16	17	18	19
14	3,90	2,56	3,57	3,90	1,14	1,75	4,02	1,39	3,85	2,70	2,22
71	24,68	12,18	13,10	7,79	9,09	12,28	9,77	9,72	14,42	8,11	15,24
08	6,49	5,77	4,76	5,19	2,27	2,92	9,77	4,17	2,88	2,70	1,11
55	6,49	9,62	10,71	7,79	13,64	20,47	9,77	12,50	10,58	5,41	13,85
48	41,56	30,13	32,14	24,68	26,14	37,43	33,33	27,78	31,73	18,92	32,41
24	—	0,64	—	—	—	—	0,57	1,39	—	—	0,83
48	—	0,64	1,19	—	—	—	—	—	—	—	0,28
24	—	—	—	—	—	—	—	—	—	—	0,28
—	—	—	—	1,30	—	0,58	—	—	—	—	0,28
—	—	—	—	—	—	—	—	1,39	—	—	0,28
95	—	1,28	1,19	1,30	—	0,58	0,57	2,78	—	—	1,94
48	1,30	1,28	—	—	—	1,17	—	—	—	—	0,28
85	1,30	7,05	8,33	10,39	5,68	5,85	2,87	5,56	8,65	8,11	6,65
—	—	—	—	—	—	0,58	1,15	1,39	1,92	—	1,39
—	—	—	—	—	—	—	—	—	0,96	—	—
—	—	—	—	—	—	—	—	—	—	—	0,28
19	1,30	1,92	—	1,30	1,14	0,58	—	—	0,96	—	0,83
43	1,30	1,28	—	2,60	1,14	0,58	0,57	1,39	1,92	2,70	1,94
95	1,30	2,56	2,38	2,60	—	1,17	2,30	2,78	3,85	2,70	3,05
14	1,30	3,85	5,95	3,90	3,41	3,51	2,30	1,39	—	2,70	2,22
66	1,30	4,49	5,95	11,69	12,50	12,28	6,32	8,33	6,73	8,11	6,65
38	—	0,64	2,38	1,30	1,14	0,58	0,57	—	0,96	—	0,28
24	1,30	—	—	—	1,14	0,58	0,57	1,39	0,96	—	0,28
71	—	1,92	2,38	1,30	—	0,58	0,57	—	—	—	—
64	28,57	17,31	11,90	7,79	4,55	3,51	13,22	4,17	3,85	2,70	5,26
48	2,60	—	2,38	2,60	2,27	1,17	2,30	2,78	0,96	2,70	1,39
93	11,69	17,31	16,67	15,58	25,00	17,54	19,54	18,06	17,31	24,32	19,94
51	5,19	8,97	8,33	12,99	15,91	12,28	13,79	22,22	19,23	27,03	15,24
57	58,44	68,59	66,67	74,03	73,87	61,99	66,09	69,44	68,27	81,08	65,65
421	77	156	84	77	88	171	174	72	104	37	361

Pleistocene Robberg industry underlies shell-midden deposits associated with the Holocene Albany and Wilton industries.

Two Robberg levels, YSL and YGL, produced good microfaunal samples (Table 6). These were accumulated between about 18 000 B.P. and 12 000 B.P. (Klein 1972a: 203). As such they are interesting because no other samples of this age have yet been found on the coast. On the other hand, their usefulness for palaeoenvironmental interpretation is reduced by the fact that they do not form part of a sequence and cannot, therefore, provide evidence of changing conditions over a period of time.

TABLE 4

Percentage representation of species in samples from Byneskranskop 1.

	1	2	3	4	5	6	7	8	9A	9B	10	11	12	13	14	15	16	17	18	19
INSECTIVORA																				
<i>C. asiatica</i>	2,70	—	—	3,33	1,41	1,92	3,05	2,19	2,14	3,90	2,56	3,57	3,90	1,14	1,75	4,02	1,39	3,85	2,70	2,22
<i>E. edwardi</i>	—	—	—	1,67	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>M. varius</i>	13,51	8,70	—	10,00	17,46	20,08	19,08	18,56	19,71	24,68	12,18	13,10	7,79	9,09	12,28	9,77	9,72	14,12	8,11	18,74
<i>S. varilla</i>	4,05	—	—	1,67	5,65	7,42	9,92	7,61	—	6,49	—	4,76	5,19	2,27	2,92	9,77	4,17	2,36	2,70	1,11
<i>C. cyanea</i>	—	4,35	—	1,67	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>C. flavescens</i>	14,86	13,04	20,00	16,67	12,58	14,01	8,40	10,91	8,55	6,49	9,62	10,71	7,79	13,64	20,47	9,77	12,50	10,58	5,41	13,85
sub-total	35,14	26,09	20,00	35,00	37,10	43,41	40,46	39,34	38,48	41,56	30,13	32,14	24,68	26,14	37,43	33,33	27,78	41,73	38,92	32,41
CHIROPTERA																				
<i>R. clivus</i>	1,35	—	—	1,67	0,26	0,55	—	—	0,24	—	0,64	—	—	—	—	0,57	1,39	—	—	0,83
<i>R. capensis</i>	1,35	4,35	—	3,33	0,26	—	0,76	1,09	0,48	—	0,64	1,19	—	—	—	—	—	—	—	0,28
<i>M. tricolor</i>	—	—	—	—	0,13	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>E. hottentotus</i>	—	—	—	—	0,13	—	—	—	0,24	—	—	—	—	—	—	—	—	—	—	0,28
<i>E. capensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	1,30	—	0,58	—	—	—	—	0,28
<i>M. schreibersi</i>	—	—	—	—	0,26	0,27	—	0,55	—	—	—	—	—	—	—	—	1,39	—	—	0,28
sub-total	2,70	4,35	—	5,00	1,03	0,82	0,76	1,84	0,95	—	—	1,28	1,19	1,30	—	0,58	0,57	2,78	—	1,94
RODENTIA																				
<i>C. hottentotus</i>	—	—	—	—	0,64	—	0,76	—	0,48	1,30	1,28	—	—	—	1,17	—	—	—	—	0,28
<i>G. capensis</i>	8,11	21,74	40,00	10,00	4,62	5,22	7,63	3,28	2,85	1,30	7,05	8,33	10,39	5,68	5,85	2,87	5,56	8,65	8,11	6,65
<i>A. subspinosus</i>	—	—	—	—	0,39	0,27	—	0,55	—	—	—	—	—	—	0,58	1,15	1,39	1,92	—	1,39
<i>A. namaquensis</i>	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0,96	—	—
<i>D. inornatus</i>	—	—	—	—	—	0,27	—	—	—	—	—	—	—	—	—	—	—	—	—	0,28
<i>M. minutoides</i>	1,35	—	—	—	1,41	0,55	0,76	2,19	1,19	1,30	1,92	—	1,30	1,14	0,58	—	—	0,96	—	0,83
<i>P. verreauxi</i>	4,05	—	—	—	—	—	—	2,73	1,43	1,30	1,28	—	2,60	1,14	0,58	0,57	1,39	1,92	2,70	1,94
<i>R. pumilio</i>	5,41	8,70	20,00	1,67	2,57	1,65	0,76	2,19	0,95	1,30	2,56	2,38	2,60	—	1,17	2,30	2,78	3,85	2,70	3,05
<i>M. albicaudatus</i>	5,41	4,35	—	5,00	3,98	3,30	1,53	3,18	2,14	1,30	3,85	5,95	3,90	3,41	3,51	2,30	1,39	—	2,70	2,22
<i>T. afra</i>	5,41	8,70	—	5,00	3,72	1,65	3,82	1,84	1,66	1,30	4,49	5,95	11,69	12,50	12,28	6,32	8,33	6,73	8,11	6,65
<i>D. melanotis</i>	1,35	—	—	—	1,80	0,82	1,53	1,84	2,38	—	0,64	2,38	1,30	1,14	0,58	0,57	—	0,96	—	0,28
<i>D. mesomelas</i>	—	—	—	—	0,26	0,82	0,76	0,55	0,24	1,30	—	—	—	1,14	0,58	0,57	1,39	0,96	—	0,28
<i>?Dendromys</i>	1,35	—	—	—	—	—	—	0,55	0,71	—	1,92	2,38	1,30	—	0,58	0,57	—	—	—	—
<i>S. krebsi</i>	13,51	8,70	—	11,67	20,41	19,51	19,08	23,50	30,64	28,57	17,31	11,90	7,79	4,55	3,51	13,22	4,17	3,85	2,70	5,26
<i>O. laminatus</i>	—	—	—	—	0,90	0,82	0,76	0,55	0,48	2,60	—	2,38	2,60	2,27	1,17	2,30	2,78	0,96	2,70	1,39
<i>O. saundersae</i>	9,46	4,35	—	11,67	12,07	12,91	12,21	9,25	10,93	11,69	17,31	16,67	15,58	25,00	17,54	19,54	18,06	17,31	24,32	19,94
<i>O. irratus</i>	6,76	13,04	20,00	11,67	5,52	5,49	6,11	7,10	4,51	5,19	8,97	8,33	12,99	15,91	12,28	13,79	22,22	19,23	27,03	15,24
sub-total	62,16	69,57	60,00	60,00	61,87	55,77	58,78	59,02	60,57	58,44	68,59	66,67	74,03	73,87	61,99	66,09	69,44	68,27	81,08	65,65
N =	74	23	5	60	779	364	131	183	421	77	156	84	77	88	171	174	72	104	37	361

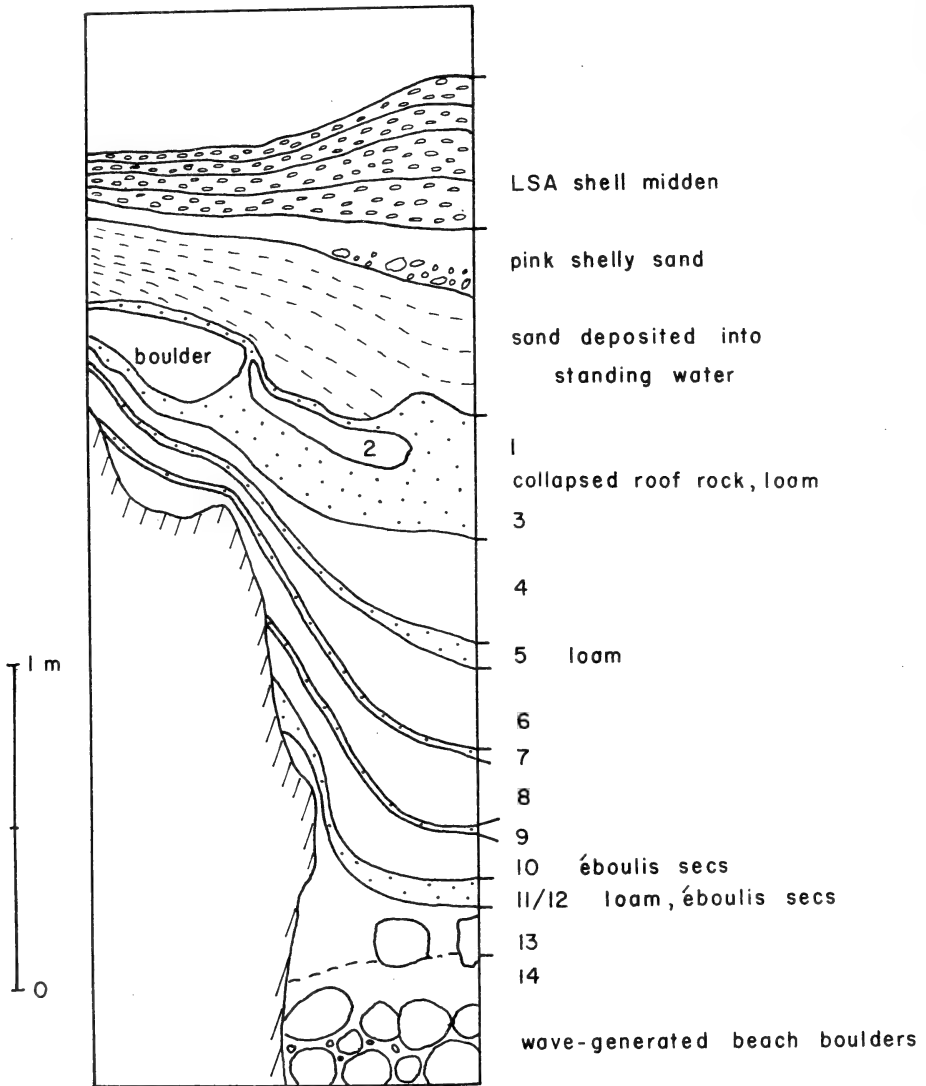
on this work. The lower half of the sequence consists mainly of iron humate-stained loams while the upper half comprises mainly shell material in a sandy loam matrix. M.S.A. material was found in the lower third of the deposits below a rubble horizon which Klein (1972a: 184; 1974a: 272) considered at one time to have been accumulated during a period of about 10 000–15 000 years when the cave was not occupied. The existence of comparable industries at Nelson Bay Cave and at Klasies River Mouth suggests, however, that the Nelson Bay Cave M.S.A. occupation might have lasted from about 120 000 B.P. to perhaps 90 000 B.P. Above the rubble horizon, the late Upper

Pleistocene Robberg industry underlies shell-midden deposits associated with the Holocene Albany and Wilton industries.

Two Robberg levels, YSL and YGL, produced good microfaunal samples (Table 6). These were accumulated between about 18 000 B.P. and 12 000 B.P. (Klein 1972a: 203). As such they are interesting because no other samples of this age have yet been found on the coast. On the other hand, their usefulness for palaeoenvironmental interpretation is reduced by the fact that they do not form part of a sequence and cannot, therefore, provide evidence of changing conditions over a period of time.

MODERN SITES

Where possible, comparative modern samples were collected from close to the archaeological sites. The Congo valley provided a wealth of material from two main sites and one minor locality, namely Boomplaas, Nooitgedacht, and Osgat respectively. A sample was obtained from Byneskranskop but, apart from this, the nearest collections to Die Kelders 1 were made at Stanford. This



1-14 MSA levels

Fig. 5. Stratigraphy of Die Kelders 1 (after Tankard & Schweitzer 1974).

TABLE 5
Percentage representation of species in samples from Die Kelders 1.

	LSA 12	MSA 1	2	3	4	5	6	7	8	9	10	11	12	13	14
INSECTIVORA															
<i>C. asiatica</i>	.	3.23	—	4.68	3.84	4.02	3.22	3.46	5.13	3.79	4.49	2.91	4.52	4.44	4.21
<i>M. varius</i>	.	29.11	7.46	35.44	33.40	38.47	28.46	30.58	27.93	28.34	28.17	33.52	22.58	16.67	12.63
<i>S. varilla</i>	.	3.80	2.99	4.16	10.71	9.52	10.44	13.33	11.29	8.98	11.90	13.11	5.16	3.33	8.42
<i>C. flavescens</i>	.	6.33	—	0.87	0.29	0.31	0.48	0.37	0.41	1.00	0.67	0.55	1.29	4.44	4.21
sub-total	.	43.04	19.35	10.45	45.15	48.24	52.32	42.60	47.75	42.12	45.23	50.09	33.55	28.89	29.47
CHIROPTERA															
<i>R. elvovus</i>	.	2.53	4.48	0.61	0.24	0.12	0.18	0.54	0.31	—	0.56	0.36	—	1.11	—
<i>R. capensis</i>	.	2.53	—	0.09	—	—	—	—	—	—	—	—	—	—	—
<i>M. tricolor</i>	.	1.27	—	0.26	0.16	0.19	0.12	0.33	0.10	—	0.22	0.18	0.65	1.11	—
<i>E. hottentotus</i>	.	—	—	0.09	—	—	—	—	0.10	—	—	—	0.65	—	—
<i>E. capensis</i>	.	—	—	—	0.03	0.06	—	—	—	—	—	—	—	—	—
<i>M. schreibersi</i>	.	—	—	0.09	—	0.06	0.06	0.04	0.10	0.20	0.11	—	—	—	—
sub-total	.	6.33	5.38	1.13	0.43	0.43	0.36	0.92	0.62	0.20	0.90	0.55	1.29	2.22	—
RODENTIA															
<i>G. capensis</i>	.	1.08	—	0.35	0.32	0.19	0.36	0.17	0.21	0.20	0.22	0.55	0.65	—	1.05
<i>A. subspinosus</i>	.	2.15	1.49	0.87	1.60	0.93	0.95	1.00	1.23	1.20	0.90	0.91	1.94	1.11	1.05
<i>D. incomtus</i>	.	—	1.49	0.09	0.11	0.06	0.06	0.04	0.10	0.20	—	0.19	—	—	—
<i>M. minutoides</i>	.	—	1.49	0.95	2.40	1.98	2.57	2.37	2.16	3.19	1.80	2.37	0.65	—	2.11
<i>P. verreauxi</i>	.	5.38	8.96	2.69	2.08	2.04	2.45	2.17	2.05	2.99	3.82	2.55	5.16	2.22	1.05
<i>R. pamilo</i>	.	3.23	5.97	4.07	3.01	3.09	4.30	4.12	3.59	5.59	5.27	5.10	6.45	2.22	6.32
<i>M. albicaudatus</i>	.	1.27	—	0.26	0.13	0.25	0.12	0.12	0.10	0.20	0.22	0.18	2.58	2.22	8.42
<i>T. afra</i>	.	30.11	25.37	15.34	11.69	13.05	13.25	12.25	11.40	15.37	12.01	11.11	21.94	18.89	22.11
<i>D. melanotis</i>	.	2.53	1.49	0.69	1.44	1.18	2.27	1.46	2.77	1.80	1.68	1.82	1.29	—	1.05
<i>D. mesomelas</i>	.	—	2.99	0.43	0.53	0.43	1.13	0.87	1.23	0.60	0.45	0.91	0.65	1.11	—
<i>?Dendromus</i>	.	—	—	2.25	7.03	4.45	7.88	6.00	6.67	5.39	6.40	4.37	1.29	1.11	1.05
<i>S. krebsi</i>	.	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>O. laminatus</i>	.	—	—	0.43	0.11	0.06	0.06	0.04	—	0.20	—	—	—	—	—
<i>O. saundersae</i>	.	2.53	—	3.99	5.30	5.19	7.70	7.70	6.37	7.19	7.74	4.74	5.81	17.78	12.63
<i>O. irroratus</i>	.	11.39	29.03	35.82	21.32	15.58	13.96	13.21	16.74	13.57	13.36	14.57	16.77	22.22	13.68
sub-total	.	50.63	75.27	85.07	53.73	51.33	47.25	57.04	51.33	54.62	53.87	49.36	65.16	68.89	70.53
N =	.	79	93	67	1154	3754	1617	2400	974	501	891	549	155	90	95

latter material was obtained by other workers and was not examined personally by the writer. The most easterly collection was made at Glentyre near Wilderness. In this case the aim was to sample a different environment, namely Knysna forest bordering lakes and coastal dunes, rather than to collect close to an archaeological site.

Again the sites are described below in alphabetical order. Some indication is given of the vegetational setting as well as of the samples collected.

Boomplaas B and C (BPB and BPC)

Boomplaas B and C (33°23'S 22°11'E) are adjacent rock shelters set in the same cliff as, and within 100 m of, Boomplaas A which is described above

TABLE 6

Percentage representation of species in samples from Klasies River Mouth 1A and Nelson Bay Cave.

	KRM1A 15	KRM1A 32	NBC YSL	NBC YGL
INSECTIVORA				
<i>C. duthiae</i>	—	—	0,28	0,26
<i>A. hottentotus</i>	0,95	0,93	—	—
<i>M. varius</i>	2,86	0,93	1,87	1,55
<i>S. varilla</i>	—	—	0,52	0,13
<i>C. cyanea</i>	—	—	0,03	—
<i>C. flavescens</i>	11,43	5,61	3,92	3,62
sub-total	15,24	7,48	6,63	5,56
CHIROPTERA				
<i>R. clivosus</i>	0,95	—	0,03	—
<i>R. capensis</i>	0,95	—	—	0,13
<i>?Eptesicus</i>	—	—	—	0,13
<i>M. schreibersi</i>	—	—	—	0,13
sub-total	1,90	—	0,03	0,39
RODENTIA				
<i>C. hottentotus</i>	2,86	2,80	1,63	3,10
<i>G. capensis</i>	4,76	4,67	1,53	1,68
<i>D. incommutatus</i>	2,86	—	0,07	0,26
<i>M. minutoides</i>	—	—	0,03	—
<i>P. verreauxi</i>	4,76	—	0,21	0,52
<i>R. pumilio</i>	5,71	2,80	0,59	0,91
<i>M. albicaudatus</i>	—	—	9,40	8,15
<i>T. afra</i>	—	—	25,70	22,51
<i>D. melanotis</i>	0,95	—	0,31	0,26
<i>O. laminatus</i>	7,62	11,21	0,35	1,16
<i>O. saundersae</i>	21,90	13,08	50,12	50,19
<i>O. irroratus</i>	31,43	57,01	3,09	3,49
<i>O. unisulcatus</i>	—	—	0,31	1,81
<i>G. ocularis</i>	—	0,93	—	—
sub-total	82,86	92,52	93,34	94,05
N =	105	107	2883	773

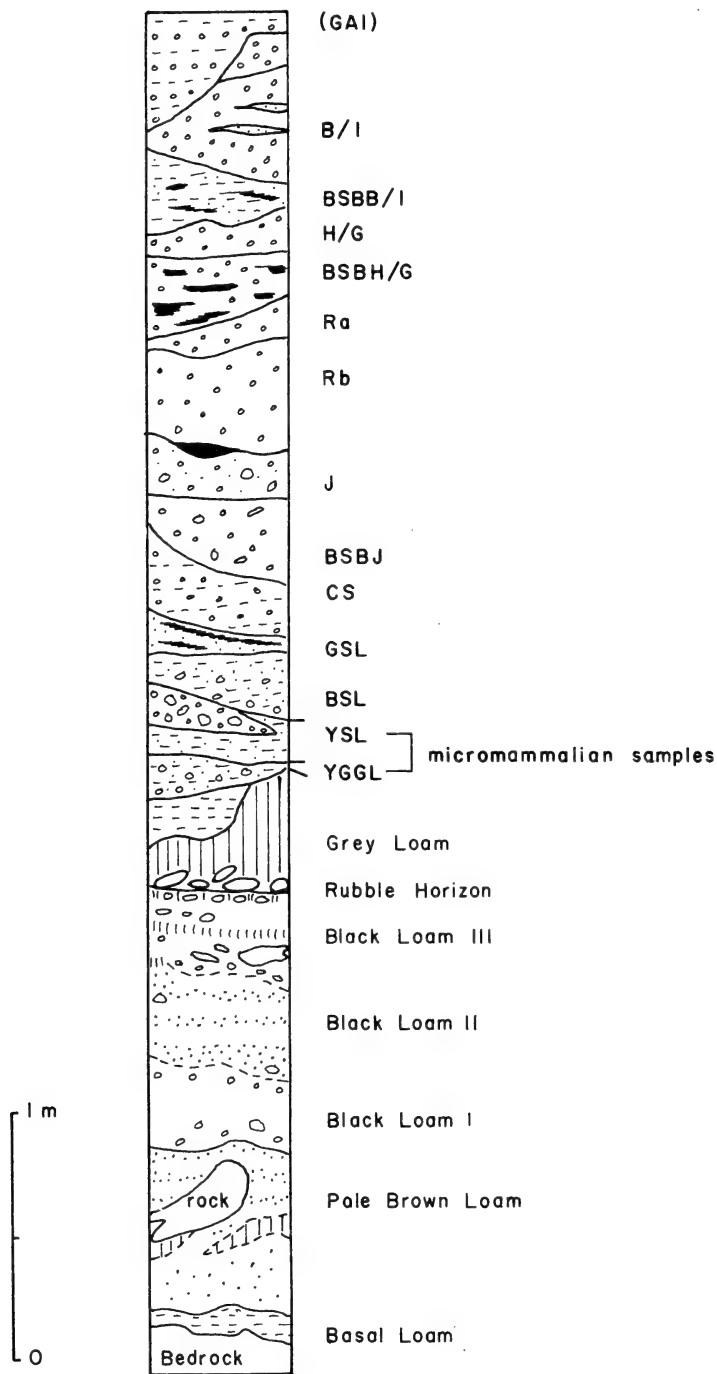


Fig. 6. Stratigraphy of Nelson Bay Cave (after Butzer 1973).

(Fig. 2). They are about 50 m above the valley floor. The surrounding vegetation is Limestone Vegetation with Mixed Bush (Moffett & Deacon 1977: 130), with some large trees near the Grobbelaars River and cultivation on the valley floor. Only the loose surface-material of these shelters was examined; it is consequently not possible to tell what depth of deposit there might have been under the surface. The surface material largely comprised *Procavia capensis* (rock hyrax or dassie) dung, supplemented to a certain extent by that of *Papio ursinus* (chacma baboon). Owl pellets were scattered throughout the shelters, although there was a tendency in Boomplaas B towards a concentration nearer what was presumably the roost. There was also a trail of pellets on various ledges below what appeared to be the roost, judging by the quantity of droppings found there. In Boomplaas C, perhaps because the area was more exposed, there seemed to be no consistent roosting-spot, although half the first collection was made from a ledge some 5 m above the main floor. The owl which frequents these shelters has been identified by G. Avery (1976 pers. comm.) as *Tyto alba* (barn owl) on the basis of shed feathers collected in the shelters. Both *T. alba* and *Bubo africanus* (spotted eagle owl) have been seen in the valley (H. J. Deacon 1976 pers. comm.). Other birds such as *Onychognathus morio* (red-winged starling) and *Columba guinea* (Cape rock-pigeon) inhabit the rocks around the shelters.

Owl pellets were collected by the writer from these shelters in January and July 1976 and 1977, the site being cleared on each occasion. Other collections have, however, been made since 1974 and some pellets have also been collected from Boomplaas A (H. J. Deacon 1976 pers. comm.). From these a sample of 50 pellets was analysed by V. A. Scott, together with a sample from Boomplaas A level OLP2, in a student project that represented an early attempt to assess the use of micromammalian remains in palaeoenvironmental studies. These samples were subsequently re-examined by the writer and the results incorporated in the present study. A bulk sample was also collected from the floor of each of the two shelters. Table 7 lists the total from these rock shelters.

Byneskranskop 2 (BNK2)

Byneskranskop 2 (34°35'S 19°28'E) is a rock shelter situated just below and in the same cliff as Byneskranskop 1, which is described above (Fig. 2). In the vicinity of the cave, both on the hillside and along the nearby Uilenkraal River, coastal scrub (Taylor 1978: 213) with *Sideroxylon inerme* (milkwood) occurs. Further patches of similar scrub also occur some 4 km north-west of the site (Schweitzer & Wilson 1978). Vegetation along the river is dense and includes *Phragmites* reeds, rushes, and alien *Acacia* species. The vegetation of the sandstone hills is predominantly restioid, whereas that on the limestone ridges is mainly proteoid (Schweitzer & Wilson 1978). Considerable areas below the rock shelter and, particularly, on the coastal plain, have been farmed and are either under cultivation or lying fallow. Elsewhere expanses of alien *Acacia*, coastal fynbos and some grassland contribute to the mosaic.

TABLE 7

Percentage representation of species in modern samples.

	BPB-C	BNK2	GLEN	NGA-B
INSECTIVORA				
<i>C. asiatica</i>	—	2,38	—	—
<i>C. duthiae</i>	1,19	—	2,19	0,98
<i>A. hottentotus</i>	—	0,13	0,73	—
<i>E. edwardi</i>	0,48	0,13	—	0,25
<i>M. varius</i>	19,21	9,14	7,83	24,02
<i>?Myosorex</i>	—	0,75	—	—
<i>S. varilla</i>	1,83	9,51	4,01	1,96
<i>C. cyanea</i>	4,60	1,75	—	2,21
<i>C. flavescens</i>	0,40	3,13	1,46	0,49
<i>Crocidura</i> sp.	—	—	—	0,12
sub-total	27,70	26,91	16,21	30,02
CHIROPTERA				
<i>N. thebaica</i>	0,08	—	—	—
<i>R. capensis</i>	0,08	0,25	—	0,37
<i>M. tricolor</i>	0,08	—	0,36	0,12
<i>E. hottentotus</i>	0,16	—	—	—
<i>E. capensis</i>	0,16	0,13	0,55	0,12
<i>M. schreibersi</i>	—	—	0,18	—
Chiroptera indet.	—	—	0,18	—
sub-total	0,56	0,38	1,28	0,61
RODENTIA				
<i>C. hottentotus</i>	1,51	—	—	0,61
<i>G. capensis</i>	—	6,26	5,10	—
<i>A. subspinosus</i>	1,83	0,75	—	5,27
<i>A. namaquensis</i>	11,59	2,63	—	13,36
<i>D. incommisus</i>	—	0,13	—	0,25
<i>M. minutoides</i>	8,81	11,39	9,84	4,29
<i>P. natalensis</i>	17,70	—	—	5,51
<i>P. verreauxi</i>	1,83	4,88	0,73	8,46
<i>R. rattus</i>	—	1,00	0,73	—
<i>R. pumilio</i>	4,44	7,26	3,28	2,33
<i>M. albicaudatus</i>	0,16	0,13	—	0,12
<i>T. afra</i>	—	7,76	—	—
<i>D. melanotis</i>	3,17	2,75	1,82	1,35
<i>D. mesomelas</i>	1,35	2,00	6,38	1,59
<i>?Dendromus</i>	—	4,63	—	1,35
<i>S. krebsi</i>	0,16	4,01	—	—
<i>S. campestris</i>	1,43	—	—	0,61
<i>O. laminatus</i>	0,63	0,63	0,91	0,86
<i>O. saundersae</i>	5,40	0,63	0,36	4,04
<i>O. irroratus</i>	11,67	15,89	53,37	19,00
<i>G. ocularis</i>	0,08	—	—	0,37
sub-total	71,75	72,72	82,51	69,36
N =	1260	799	549	816

There were no fresh pellets in the shelter, only a concentration of micromammalian bones which was particularly noticeable on the northern side of the shelter. A bulk sample (Table 7) was collected from this area, but it was not possible to examine the shelter in any detail as it was occupied by a swarm of bees.

Glentyre Shelter (GT)

Glentyre Shelter (33°59'S 22°38'E) is located about 100 m off the road which skirts the north-east corner of Onder-Langvlei and approximately 6 km east of Wilderness (Fig. 1). The rock shelter, which is an archaeological site excavated by A. J. H. Goodwin in 1938–40, published by Fagan (1960) and mentioned by Schrire (1962), is situated about 100 m above lake-level on the side of the ridge bounding the string of lakes to the north. The shelter is situated in Knysna forest, while the lower ground is cultivated and the lake is surrounded by *Phragmites* reeds. The owls (*Tyto alba*) appear to roost on a ledge north-east of, and above, the shelter. The result is that, when not caught in vegetation, the pellets roll and are washed down the slope into the nearer half of the shelter. There were a great number of micromammalian bones both here and on the talus slope below the shelter (Table 7). This fact, in itself, throws some interesting light on the mechanics of accumulation of these bones in archaeological sites.

Nooitgedacht A–C (NGA–C)

Nooitgedacht A–C (33°22'S 22°10'E) are adjacent caves and shelters situated 2,5 km north-west of Boomplaas about 100 m above the valley floor (Fig. 2) in a Limestone Vegetation area. Nooitgedacht A is by far the largest of the caves and seems to be the main roost since most of the material has come from there. It consists of a main cave with an elevated tunnel or fissure extending back at least 20 m from the northern corner of the cave. On the second visit, pellets were collected from this tunnel so that it is clear that the owls roosted far up it at least part of the time. Nooitgedacht B and C are very small shelters or overhangs. As at Boomplaas, the main surface material comprises *Procapra capensis* dung together with some faeces of *Papio ursinus*. *Onychognathus morio* and *Columba guinea* inhabit nearby rocks as they do at Boomplaas. The bodies of three *Tyto alba* have been found in the cave.

In January and July 1977 collections were made at Nooitgedacht where the main cave, A, yielded a great deal of material. Caves B and C yielded a few pellets each and were presumably used only as occasional alternative roosts to Nooitgedacht A. Nooitgedacht B did, however, provide a useful bulk sample. The total for caves A and B is given in Table 7.

Osgat (OG)

Osgat (33°22'S 22°11'E) lies 1,3 km north-east of Nooitgedacht and 5 km north of Boomplaas, only just above the valley-floor (Fig. 2). It is a small shelter with a cleft in the rock parallel to the back wall in which the pellets were

found. The shelter was obviously well used; not only were there *Procapra capensis* and *Papio ursinus* droppings but also those of domestic cattle. Bats were found roosting in the cleft and it was interesting that the owl pellets contained an unusually high proportion of bat remains. These remains were identified as belonging to *Nycteris thebaica* (Egyptian slit-faced bat) and, although it was not possible to identify the live specimens, it is likely that they were the same species. Osgat yielded only a few pellets in January 1976, and since the site was obviously deserted it was not visited again.

Stanford (ST)

Stanford village (34°26'S 19°28'E) is situated about 15 km south-east of Hermanus beyond the head of the Hermanus lagoon. The material which was published by Grindley *et al.* (1973), but is no longer available (C. J. Vernon 1977 pers. comm.) was recorded as having been collected from 'a hole 3 m above the river in the bank of the Klein River, about 1.5 km west of Stanford', that is, towards the lagoon (Fig. 1). 'The surrounding habitat was a fringe of *Phragmites* and macchia along the river encompassed by agricultural lands, rooikrans thickets and gum plantations' (Grindley *et al.* 1973: 266). (It should be noted that 'macchia' has been called coastal fynbos in the present study on the basis of current nomenclature.)

The second collection in the area was made at Windheuvel (34°28'S 19°32'E) which is about 8 km east-south-east of Stanford (Fig. 1). The roost was in a hole in a limestone cliff along a tributary of the Modder River, which itself drains into the Klein River. Unfortunately an attempt to relocate the site at a later date failed and it was thought that the cliff must have partly collapsed. The material from this collection is being held privately by T. N. Pocock of Vanderbijl Park, who provided the writer with a copy of his analysis.

THE MATERIAL

The material consists of large quantities of bones of rodents and insectivores, together with a small number of bat remains. The identity of the agent responsible for their collection is first considered. Thereafter, the methods used to collect the samples and questions of identification are discussed. Finally, the relationship of the excavated sample to the original living community from which it was derived, as well as the type of interpretations it is possible to make therefrom, is examined.

AGENCY OF ACCUMULATION

It has generally been assumed (Cartmill 1967: 171) that owls are responsible for the accumulation of quantities of microfaunal remains in caves. While this does, indeed, seem to be the most likely explanation, it is as well to consider the question in rather more detail in order to ascertain whether or not other small predators might have been responsible. Given the large numbers of

small animals and diversity of species involved, it seems reasonable to accept that the majority of the microfauna was accumulated in the cave by some outside agency. A few animals such as bats might have been living in the caves and have died there, but this cannot have been true for most of the animals which would not live in or enter a cave voluntarily. For instance, limited trapping at Boomplaas A produced only one species, *Aethomys namaquensis*, in March 1979. Nor can it account for the quantities of animals involved. It is then necessary to employ a process of elimination in order to isolate the agency responsible. Firstly, only predators can be involved. Secondly, only predators of a certain size would be likely to catch animals in the size-range represented, that is, anything up to the size of a half-grown *Georychus capensis* (Cape mole-rat). Small carnivores such as *Herpestes pulverulentus* (Cape grey mongoose) are a possibility, as are various birds such as owls and eagles. Humans are also known to eat rodents. Shortridge (1934: 240) notes that in summer the Okavango of Botswana catch and eat large quantities of *Otomys irroratus* (vlei-rat) and *Dasymys incommutus* (shaggy swamp-rat), as well as the much larger *Thryonomys* sp. (cane-rat). Vesey-Fitzgerald (1964: 66) records the fact that the Wanyika of Tanzania catch and eat *Rhabdomys pumilio* (striped field-mouse) which is surprisingly small. Also small is *Steatomys pratensis* (fat mouse) which Coetzee (1971: 2) records as being eaten throughout its range. Lizards, frogs, tortoises and insects are also said to be eaten on occasion by Bushmen in Botswana (Schapera 1930: 141; Service 1966: 101, quoted by Yellen & Lee 1976: 42).

In the matter of eliminating the possibilities, various points may be considered. For instance, the time of day at which prey and predator are active must coincide. This line of argument may not seem very strong since two of the main prey items are apparently active throughout the twenty-four hour cycle. Davis (1973) found, however, that *Otomys irroratus* was primarily crepuscular and concluded that this activity pattern is probably common to all Otomyinae. Thomas & Schwann (1905a: 264) noted both nocturnal and diurnal activity in *Myosorex varius* (forest-shrew) but Roberts (1951: 39) stated that the Soricidae in general are nocturnal. The great majority of species represented in the samples is nocturnal and must have been taken at night. This eliminates humans who are not nocturnal and are unlikely to have developed snares capable of catching huge numbers of animals. Likewise, the diurnal raptors such as the eagles are ruled out on this ground as well as by the fact that they digest the bones of their prey (R. A. C. Jensen 1977 pers. comm.). *H. pulverulentus* is also mainly diurnal (Dorst & Dandelot 1970: 122). Of the remaining possibilities, only animals which frequent caves and regularly excrete the more or less complete bones of their prey in one cave can have been responsible. By this token the various carnivores may be ruled out. Some, such as *Canis mesomelas* (black-backed jackal), may tend to defaecate in restricted places (Stuart 1976: 204) but not in caves. This species has been shown to have a very varied diet (Stuart 1976: 201) which only sometimes includes moderate

proportions of rodents. *Felis libyca* (wild cat) and *Genetta genetta* (common genet) eat large quantities of rodents (Stuart 1977: 240; Smithers 1971: 125, 165) but, again, they would defaecate in the open and, in the latter case at least, the prey bones tend to be very broken up (Stuart 1977: 241). Possibilities are now reduced to the nocturnal birds of prey which, in practice, means the owls since only these eat small mammals in large quantities. Of these *Tyto alba* (barn-owl), *Bubo africanus* (spotted eagle-owl) and perhaps *Bubo capensis* (Cape eagle-owl) would be likely to roost in caves (McLachlan & Liversidge 1970: 246 ff). *Bubo capensis* would, however, probably take larger prey; little is known of the local race, *B. capensis capensis*, but it cannot be expected to take appreciably smaller prey than the slightly larger *B. capensis mackinderi*, which is known to eat animals the size of hares in Zimbabwe (Steyn & Tredgold 1977: 41). Although the diet of *T. alba* and *B. africanus* is similar, the pellets of the latter typically contain highly fragmentary prey remains (Grindley *et al.* 1973: 266). This finally leaves *Tyto alba* as the most likely creature to have accumulated microfaunal remains in caves. In addition, *T. alba* is known to hunt occasionally on dull days (McLachlan & Liversidge 1970: 247) which could help to account for the small proportion of diurnal species represented. A further indication is that the range of prey species in modern collections of pellets, all of which are thought to be from *T. alba*, are similar to those in the archaeological samples.

METHODS OF COLLECTION

This study was initiated after most of the archaeological material had been excavated. For this reason the collection of microfauna has taken place under differing circumstances. In some cases the excavators routinely kept the microfaunal remains which were extracted during the general sorting after the material had been screened through fairly finely-meshed sieves. A 3 mm ($\frac{1}{8}$ ") mesh was used at Nelson Bay Cave, at Die Kelders 1, and at Byneskranskop 1. This has proved adequate for the collection of microfauna. At Klasies River Mouth 1A, 12 mm ($\frac{1}{2}$ ") and 6 mm ($\frac{1}{4}$ ") mesh sieves were used for the most part and only selected samples were screened through a 1.5 mm sieve for the recovery of small finds, including microfauna. The result is that the sample from this potentially very rich site is extremely small. At Boomplaas A, the material from the test pit, square P12, was screened through a 3 mm meshed sieve and the microfauna was extracted during the general sorting, except in the case of levels OLP2 and OLP3. Here the sample was so large that it remained unsorted until the writer examined it. During the main excavation at Boomplaas A, a system of sampling for microfauna and other small finds was employed in order to speed up the process of sorting. Material from one sample square in each line of squares was screened through a 2 mm meshed sieve as opposed to the usual 3 mm meshed sieve. In the upper levels, the microfauna was sorted from all the squares although obviously more was retained by the finer screening. Thereafter it was decided that a sufficiently large sample could

be obtained from the sample squares alone and the extraction of microfauna from the other squares was discontinued.

The modern comparative material derives from both bulk samples and complete owl pellets. A bulk sample was collected from an unmeasured area at Byneskranskop 2. From both this and a similar sample from Nooitgedacht B, the bones were subsequently extracted by hand; the high proportion of bones and lack of fine matrix made sieving unnecessary. At Glentyre as much diagnostic cranial material as possible was collected from the floor of the site, care being taken not to overlook the smaller species. At Boomplaas B and C, bulk samples were collected from a measured square metre, an area which it was thought would provide an adequate sample. The area was marked out to cover places where the pellets tended to accumulate and it was assumed that there would consequently be a high proportion of bones to general matrix. This mostly comprised *Procavia capensis* (rock hyrax) dung which was whole on the surface, disintegrated below and compacted beneath that. The top two categories were collected and screened in the 2 mm meshed sieve. The bones were then extracted and the dung discarded. Pellets were first measured and weighed. They were then pulled apart when dry and the bones were extracted. This system was found to be the most efficient, although it is known that some workers prefer to soak the pellets first (Vernon 1972: 11). It was not thought necessary to develop a mechanical method such as that used by Southern (1954: 389). An account was kept of the contents of each pellet, including the presence of birds, frogs and the occasional beetle, although non-mammal material was not further considered.

IDENTIFICATION

The identification of small mammal remains from archaeological sites is hindered by the broken nature of the material. Most distinguishing characters employed by zoologists are missing. These include external characters such as colour of pelage, relative tail and body length, and numbers of mammae and internal characters such as chromosome counts. Sometimes cranial and dental characters are invoked in keys, but this is usually after basic distinction has been made on other characters not preserved under archaeological and palaeontological conditions. The need for a key based solely on cranial characters was recognized by Hanney (1962), who published such a key to the small mammals of Nyasaland (Malawi). In 1972 Coetzee published a similar key for southern Africa expressly for the identification of remains from owl pellets. Such keys are extremely useful, especially if one is dealing with complete or nearly complete skulls. Unfortunately, this is seldom the case in archaeological contexts so that the pioneer work of Davis (1965), who distinguished species by their alveolar patterns, a logical extension of the established practice of counting tooth roots, is of great importance. More recently Knox (1976) has examined the alveolar patterns of Muridae in Australia. Misonne's (1969) comprehensive study of the Muridae is based on the teeth and as such can be usefully employed.

In practice it was found that distributional data such as those of Davis (1974), Meester (1958, 1961, 1963), and Coetzee (1972) gave a basic indication of the species likely to occur in the southern Cape. It is emphasized, however, that this merely provides a starting point; it is in no way considered to be rigidly inclusive or exclusive since there is, after all, every reason to believe that changes in distribution have taken place (Meester 1958; Brain & Meester 1964; Avery 1977). Subsequently a key such as that of Coetzee (1972) is useful for identifying the more obvious species and perhaps for eliminating other possibilities.

Although it is possible to identify definitely the majority of specimens, there remain certain cases where doubt is likely to arise, particularly in closely related species. The following remarks refer to such areas of possible confusion:

1. *Praomys* spp. and *Saccostomus campestris*

The mandible of *S. campestris* may be distinguished from those of *Praomys* spp. by the facts that the body is relatively much deeper and that the anterior border of the muscle attachment is not contiguous with the mental foramen as it is in *Praomys*. It was not found possible to distinguish the mandible of *P. natalensis* from that of *P. verreauxi* with any degree of certainty. The teeth of the latter are relatively smaller than those of the former, but that is not a distinguishing factor due to overlapping ranges.

2. *Acomys subspinosus* and *Steatomys krebsi*

Because the region of M_3 is frequently broken, it is often necessary to resort to other characters to distinguish the two species. For instance, *Acomys* has a broad zygomatic process and no masseter knob, whereas *Steatomys* has a narrower zygomatic process and a masseter knob; the anterior palatal foramina penetrate between the roots of the upper first molars in *Steatomys* but not in *Acomys*. Several differences are apparent when the mandible is viewed in the buccal aspect. In *Acomys* the anterior border of the muscle attachment is level with the anterior alveolus of M_1 and is, therefore, situated closer to the mental foramen than is the case in *Steatomys*, where the anterior border of the muscle attachment is level with the midpoint between the two alveoli of M_1 . In *Acomys* the symphysis forms a visible angle with the ventral border, which itself forms an almost straight line. In *Steatomys*, on the other hand, the junction of the symphysis with the ventral border is not visible but is, instead, incorporated in the general curve of that border.

3. *Dendromus* spp. and *Mus minutoides*

Davis's (1965: 145) potentially useful point that *M. minutoides* possesses a three-rooted M_2 should have provided the key to distinguishing the mandible of this species from those of *Dendromus* spp. Unfortunately, however, it was

found that this feature was not constant in the material examined. While it seems that the posterior alveolus of M_2 in *M. minutoides* is at least broader than the corresponding alveolus in *Dendromus*, this fact is not demonstrable with any degree of certainty. Consequently, where doubt existed, the specimens were assigned to the category ?*Dendromus* as these species generally occurred with greater frequency. It is implicit in the above that the mandibles of the two species of *Dendromus* were also indistinguishable when the teeth were missing.

4. *Myosorex varius* and *Crocidura cyanea*

Although it is generally possible to distinguish between these two species, there remains a small body of material that cannot be identified. This consists of the central portions of the mandible and P^4 to M^3 regions of the maxillae when the teeth are missing. In these cases, specimens were assigned to ?*Myosorex* since this genus was invariably found to be numerically superior on the basis of identified specimens.

5. *Crocidura cyanea* spp.

The only dental character given by Meester (1963: 48) to distinguish *Crocidura cyanea cyanea* from *C. c. infumata* concerns M_3 . Since this tooth is frequently missing it is rarely possible to distinguish the two subspecies in subfossil material. The only reason for attempting such a distinction is that the two subspecies live in different environments and may, therefore, be useful in the interpretation of past environments.

6. *Otomys* spp.

Identification of the various species of *Otomys* has proved difficult. The teeth are easily lost, especially the M^3 which, together with the M_1 , is the most diagnostic tooth. Moreover, there is a great deal of variability in the numbers of roots and, therefore, of alveoli. General trends are noticeable which allow assessment of specimens with reasonable but not absolute certainty. Very large specimens are likely to be *O. laminatus*, especially if there are a large number of alveoli since the number of these seems generally to be proportional to the number of laminae. In this way *O. unisulcatus*, which has fewer laminae, tends to have fewer alveoli. This latter species is, however, roughly the same size as *O. saundersae* and as such can only rarely be distinguished with any degree of certainty if the teeth are missing. The most frequently found species in most cases are *O. irroratus* and *O. saundersae*, of which the latter is considerably the smaller. There are, however, specimens of an intermediate size which must necessarily be assigned somewhat arbitrarily to one of these species and it is possible that some of the larger specimens may be *O. laminatus* and not *O. irroratus*. It is felt, however, that while the more frequent species may tend to be over-represented, the proportions are generally accurate.

THE NATURE OF EXCAVATED SAMPLES

The excavated sample bears a complex relationship to the biocoenose (life assemblage) from which it is derived. Examination of the taphonomic processes involved provides some understanding of that relationship and its consequent effects upon interpretation. It is also of importance to consider the quality of the sample in order to assess the type of deduction it is possible to make from the data. Moreover, the fact that the excavated samples generally comprise material accumulated over a considerable period of time raises a question as to the extent to which periodic natural fluctuations will be noticeable.

Depending upon the type of investigations being made, consideration of all these points may not be necessary. For instance, for the purpose of making relative environmental interpretations it may be necessary to establish the relationship of one sample to another but not to the original communities. Thus, establishment of the fact that similar biases were affecting the samples would be important but not necessarily the exact nature of those biases. If, however, an attempt were to be made to establish absolute changes in conditions with, perhaps, a quantitative approach, then the relationship of the sample to the population would become important. Equally, any work on population structure would demand such a base. In general it would appear advisable to examine such questions as an aid to better understanding of the overall subject, whether or not it has any immediate relevance.

Taphonomic factors

The theoretical sequence of events from life assemblage to the collected sample is discussed by Clark *et al.* (1967). Behrensmeyer (1975) considers the taphonomic processes involved, with particular reference to large mammals in open situations. Brain (1967) has examined differential preservation of bone near a Hottentot (Nama) village in South West Africa, as have Binford & Bertram (1977) for some American sites. Both the latter sets of data are of theoretical importance, although they are of cultural origin.

Given a life assemblage whose composition is regulated by various biotic factors (Clark *et al.* 1967), the initial factor governing which bones will be included in the deposit is the mode of death (Behrensmeyer 1975). In the present case this would appear to be almost entirely due to predation by *Tyto alba*, as has been discussed above. The possible biases caused by *T. alba* are considered below. In the present context, however, it is necessary to examine the possibility of further biases due to differential damage of the bones by the predator. In fact it appears that *T. alba* causes very little damage to small mammal bones (Grindley *et al.* 1973; pers. obs.), so it seems unlikely that this will cause any significant bias. Although *T. alba* is said to feed only the body of the prey to its young, it apparently eats the head itself (Vernon 1972: 109). There has, however, been no indication that there is any selectivity in prey fed to young birds. Failure of the adult to drop its pellet at the roost site should, therefore, have the effect of reducing numbers indiscriminately if the skulls

alone are counted. Glue (1967) noted one case of an owl not eating the head of its prey but was of the opinion that this did not happen often and that a count of skulls and mandibles gives a reliable count of prey taken. This is an important point since in the present study only mandibles and maxillae were counted. A small addition to the sample collected by the predator may be made by small mammals dying in the cave from other causes. The identity of such animals is mentioned elsewhere.

The thanatocoenose (death assemblage) thus accumulated is further reduced by factors of preservation related to weathering, transport and burial. In the present case, the fact that the bones were deposited in rock shelters or caves should have the effect of protecting them from the extremes of weathering. They will also be protected initially by being enclosed in the owl pellet which effectively reduces the period of time between exposure and burial. Transport must necessarily have been limited in the cave situation, but one real source of damage will have been trampling by people and animals. Of the taphic or burial factors listed by Clark *et al.* (1967: 117) the nature of the sediment could be relevant in the present context. It is possible, for instance, that the coarse matrix provided by shells or stone artefacts will adversely affect the preservation of small mammal bones. Similarly, a rock fall or high degree of spalling could well damage or destroy such bones. Of the post-depositional factors, the actions of burrowing animals and the effects of permeating solutions may possibly affect small mammal bones in caves. In the case of the former, however, it may be that the bones will generally tend to be disturbed rather than destroyed, although the digging of storage pits by humans could have a more serious effect. Damage by erosion within a cave is almost certainly a minor consideration, but that caused by leaching is likely to have been greater. The lighting of fires in the caves could destroy bones on or even below the surface.

In general it would seem that these various factors will act more or less indiscriminately. This is because there is relatively little variation in the size of the specimens, which suggests similar reactions to destructive forces. Some correlation of size with susceptibility to destruction or damage is suggested by both Clark *et al.* (1967) and Behrensmeyer (1975), who note that the effects of weathering are less on small bones than they are on large ones. The chances of disproportionate preservation are probably reduced in the present case by the fact that only maxillae and mandibles have been considered. In particular the body of the mandible, which is constructed of dense bone with a consequently high survival rate (Brain 1967), will perhaps have a similar chance of being preserved in animals of a similar size. It would seem, therefore, that in the present case the fossil assemblage will constitute a reasonably unbiased sample of the thanatocoenose.

Sample quality

Clark *et al.* (1967) discuss the factors responsible for the differences between the total fossil assemblage and the collection ultimately available for

interpretation. The first group of factors is connected with collecting. In the present context this could mean that there will be a bias against the smaller species either because the material was sieved through an insufficiently fine screen or because the specimens were overlooked in the subsequent sorting. Jaws which are prone to losing their teeth are also at greater risk of being overlooked. Personal biases such as training, persistence, psychological fluctuations, visual acuity and physical comfort are all considered by Clark *et al.* (1967) to affect collecting which, in this case, constitutes retrieval of the specimens from the excavated matrix. Where a group of collectors is involved even these factors will become variable, although they may balance out.

The data which are available for interpretation may be different again from the material collected. Here the factors relate to identification and the estimation of minimum numbers of individuals represented. In the present case the question of differential ease of identification (Clark *et al.* 1967: 120) does not apply because, as is explained below, each individual is represented only by its jaws. This means that all individuals are, in effect, identified at the same level despite the fact that it might have been possible to identify some species on much less evidence. Grayson (1978) has further pointed out that rare species tend to be heavily over-represented because the fewer the elements present the greater the chance that each element will represent another individual. Simpson *et al.* (1960: 116) have also noted that animals with more bones have a potentially greater chance of being represented in the sample. In the present context, however, the representation of each individual by the same four bones means that such biases are eliminated and each individual has an equal chance of being included.

Excavated samples cannot meet the usual specifications for homogeneity of faunal sampling of live populations (Simpson *et al.* 1960). They must therefore necessarily always be more heterogeneous. Thus the sexes will not usually be distinguishable and age distinctions may not always be possible. This fact could have an important bearing on attempts to interpret interpopulation differences. For instance, it will be difficult, if not impossible, to establish with certainty the cause of variation in mean individual size. The change may be due to a difference in sexual or age composition of the sample rather than to any real change caused, perhaps, by a response to climatic variation. Whilst it may be possible to control the age factor, it will not be possible, in small mammal cranial material at least, to control the sexual factor.

Neither is the available sample always of a size to represent adequately the population from which it was drawn. This means again that it is not always possible to come to reliable conclusions about the degree of similarity or difference between different populations. In another context the size of the sample may affect its composition. The question of the size of the sample necessary to include all available species is discussed below. If, as is suggested, the size of the sample must increase with the number of possible species, it follows that the number of species that may be omitted from a small sample

must also increase in relation to the possible number of species. Therefore, the absence from a small sample of a species which never forms a large proportion of any sample cannot be regarded as significant because it could be due to sampling error. Only where species normally form a large proportion of a sample may their absence be ascribed to some real change in conditions. Generally, however, presence is more significant than absence and changes in proportional representation may provide useful data for interpretation.

Levels of inference

It has been shown that some rodent populations are subject to periodic and, in some cases, spectacular fluctuations in size (Honer 1963). Such fluctuations are of a cyclical nature and may be due to a number of causes (Krebs 1972). They may occur approximately every 3 years (Honer 1963) or over longer periods such as every 8 or 10 years (Davis 1966). Moreover, trapping programmes in the south-western Cape have demonstrated that seasonal variation in population size may also occur (R. C. Bigalke 1975 pers. comm.). Other irregular fluctuations may be caused by events such as flooding (Davis 1973; Brooks 1974) or fire. The effects of the latter appear to be quite variable. In Ugandan grassland all species had returned to an area 7 months after burning and by 11 months there was little difference between the burnt and unburnt areas (Neal 1970). R. C. Bigalke (1975 pers. comm.), on the other hand, has found that in the south-western Cape a period of 3 or 4 years elapses before burnt ground is fully recolonized.

In none of these cases is the cycle of fluctuations longer than a decade. For this reason one would not expect to be able to detect evidence of such fluctuations in material from archaeological sites. This is because each excavated sample of micromammalian fauna is likely to comprise material accumulated over a period of some hundreds of years. It would seem most unlikely, therefore, that the short-term fluctuations described above will be discernible in excavated samples. The only possible exception is the effect of fire on long-term averages. This is not because the effects of each burn are long-term, but because the effects of possibly frequent burning could be cumulative. Kruger (1979) is of the opinion that natural fires in the fynbos were likely to have occurred randomly at about 6 to 30 or 40-year intervals. It is also presumably possible that the frequency might have varied at different times in the past. Moreover, fires caused by humans are likely to have become increasingly common. In the first instance, people might have fired the vegetation in order to encourage growth of geophytes (Deacon 1976: 174). Later, pasture control by burning became prevalent after the introduction of sheep into the southern Cape around 2 000 B.P. (Deacon *et al.* 1978). It seems unlikely, however, that fire will have had a differential effect on the micromammalian fauna, for two reasons. The first is that, even if the diurnal species are most likely to be reduced by fire (Neal 1970), these species are least frequently preyed upon by *Tyto alba* (see discussion below). If, however, fire may be assumed to destroy

food resources indiscriminately, then all or most species will be equally affected. The second reason is that, depending on the extent of the burn, the owl may either extend its hunting territory or move its roost temporarily. In the first case the effects of a short-term change in prey composition would probably not affect the longer-term average. In the second case the overall size of the sample and not its composition would be affected. It would appear, therefore, that such long-term fluctuations as are evident in excavated samples must have been caused by large-scale events or trends outside the range witnessed on a short-term basis.

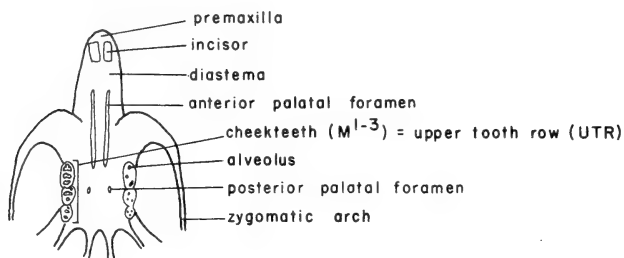
While it is clear in general that excavated samples can only monitor major trends or fluctuations, the actual size of these may vary. This is because different samples represent the average situation over varying periods of time. It is normally not possible to regulate samples so that, within a sequence, they all represent an equal period of time. This is, however, unimportant if there is some indication, preferably a suite of radiocarbon dates, of the actual or relative period of time represented. In this way it will be possible to assess the relative importance or amplitude of a trend. Thus, an isolated fluctuation shown by a sample accumulated over a period of 100 years is minor compared with a generalized trend evident over a period ten times as long.

THE NATURE OF MICROMAMMALIAN EVIDENCE

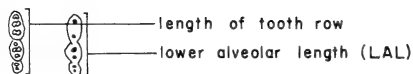
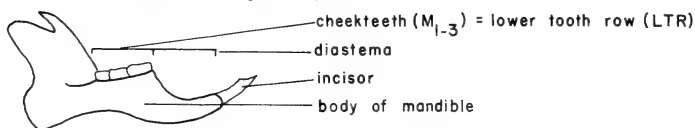
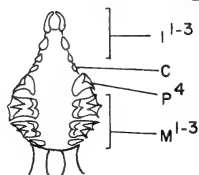
The use of micromammalian remains as evidence of environmental change requires the prior assessment of the nature and possible limitations of the evidence. In the first instance it is necessary to establish whether, in fact, the evidence can show that environmental change has taken place. Thereafter, in general terms, consideration must be given to matters relating both to the micromammals themselves and to the predators that are thought to have been responsible for accumulating the samples.

Micromammalian evidence and environmental change

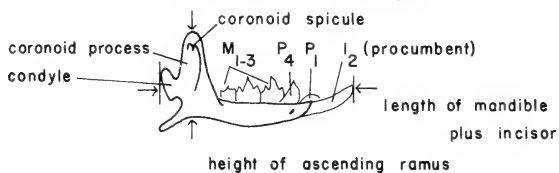
It has been assumed that micromammalian remains may be used to indicate environmental change. The validity of this assumption must now be tested. It may be, for instance, that changes in the composition of the small mammal fauna represent an autogenous succession to a stable climax such as is known to occur in plants (Krebs 1972). Cyclic change, again as observed in plants, is another possibility. At the population level, fluctuations about a mean density level are known to occur under stable environmental conditions (Klomp 1962). However, all these changes tend to operate towards the establishment of homeostasis, or a state of equilibrium, which is said to operate at all levels of the ecosystem (Odum 1971: 34). This would suggest that any extension to the regular range of fluctuation must represent disruption of the equilibrium. In other words, since climate is the overall factor controlling the vegetation of an area (Krebs 1972: 432) and animals are directly dependent on plants (Krebs 1972: 416) it follows that any unusual change in the rodent community must

Rodentia (*Proomys verreauxi*)

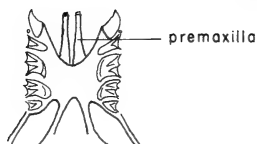
left mandible - lingual aspect

Insectivora (*Crociodura flavescens*)

right mandible - buccal aspect



0 10 mm
approx.

Chiroptera (*Rhinolophus clivosus*)

right mandible - buccal aspect

Fig. 7. Diagrams of species representative of micromammalian orders with terminology used.
(See Meester 1963 and Rosevear 1969 for further explanations.)

reflect similar change at some higher point in the chain of influence. At the same time it must also be borne in mind that not all species may react, or they may react differently at different rates, to a particular change, especially in areas of intermediate climatic change (Tchernov 1975: 346).

The type of change found in the community is not, in fact, illustrated by the subfossil small mammal material. The pattern of change does not show the progressive stages characteristic of a succession. It is to be expected that such stages would be characterized by one or more dominant species. These would be replaced or succeeded by other species after a period of time and there would not be evidence of a resurgence of a species once it had been replaced. However, the changes visible in the small mammal record (Figs. 8–9, for example) represent fluctuations which are not consistent with the succession model. Equally, there is no evidence that the changes are truly cyclic as described by Krebs (1972: 432). The data do not show that one species is regularly replaced by and, in turn, replaces another.

Two facts are observed about population density. One is that it does not rise indefinitely and the other is that it varies in different environments (Chitty 1960). This implies that there are mechanisms which prevent unrestricted increase in density and others which control mean density, all of which tend to maintain a state of equilibrium. There has been considerable discussion as to the nature of these mechanisms. It has been suggested that climate, enemies (predators, disease, etc), self-regulation or a combination of all three could be responsible (Krebs 1972: 287). It seems likely, in fact, that the dominant factor will vary depending upon the favourableness of the environment, as suggested by Huffaker & Messenger (1964, quoted by Krebs 1972: 280). Thus, in marginal areas climate may be the most important factor, whereas in optimal areas natural enemies or decline in the quality of the individual (Chitty 1960) may be responsible for regulating numbers. Equally, such mechanisms as territoriality may control numbers below a level at which the food supply would be destroyed.

It has been suggested above that the fluctuations which are visible in the subfossil record are on a scale far larger than those which occur in a stable environment. If this is the case, it would appear that the mean population densities of different species must have altered at various times in the past. Mean population density has been observed to be higher in optimal areas than in marginal areas. If, therefore, the mean population density is shown to vary from time to time in one geographical area, it must mean that the suitability of that area has varied. It would not be possible, given all the regulatory mechanisms discussed above, for such changes to occur unless a major parameter were altered. In the present case, since many of the animals are herbivorous mammals, it would appear that changes in the vegetation would have the most important effect on the favourableness of the environment. In the case of the insectivorous mammals it may be that a change in the insect fauna and/or change in the vegetation was the cause. In both cases it is to be

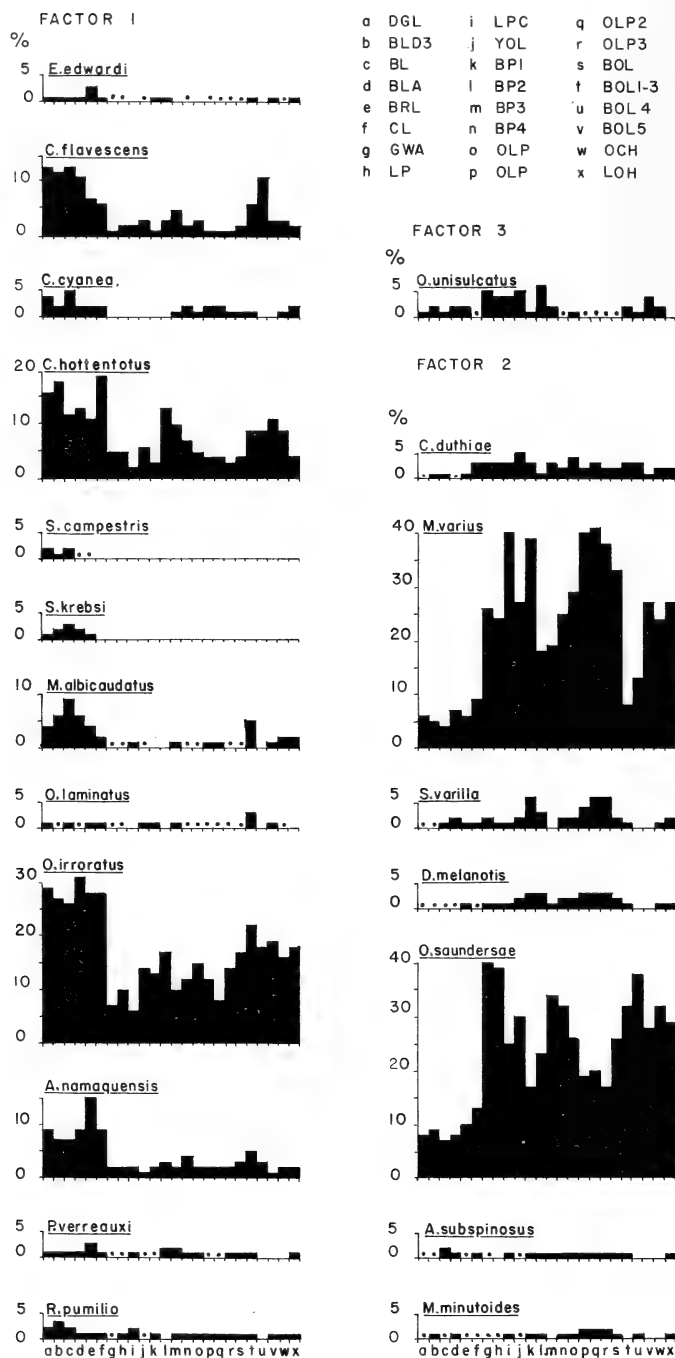


Fig. 8. Variation in percentage representation of species loading highly in the analysis of species from Boomplaas A (* = less than 0,5%).

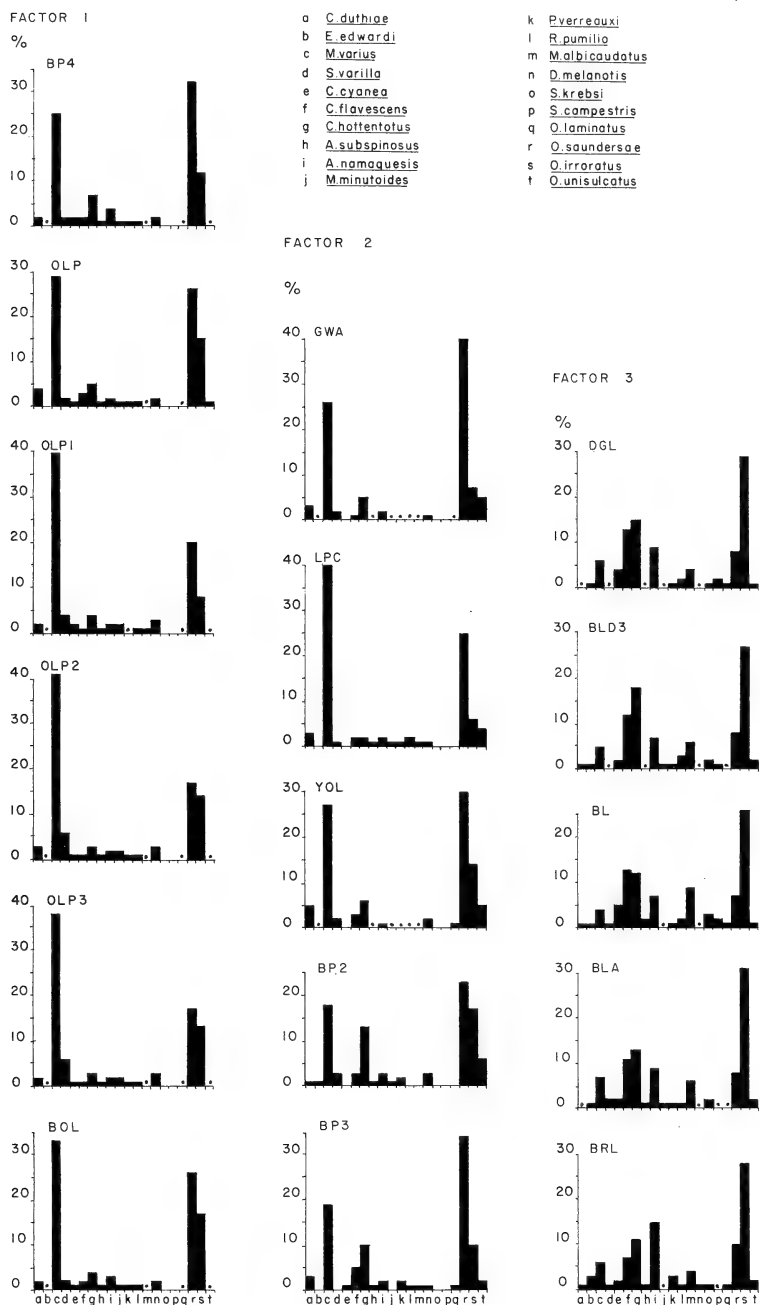


Fig. 9. Proportions of species from levels loading highly in the Varimax solution of the analysis of levels at Boomplaas A (* = less than 0,5%).

expected that a change in the climate would be the initial factor responsible for altering the quality of the environment. In fact, considerable changes are known to have occurred in the climate during the Upper Pleistocene and the Holocene, and consequent changes in the vegetation must have taken place (Van Zinderen Bakker 1976). It is these long-term changes which are most probably being reflected in changes in species composition of the micromammalian fauna. Significant variation in mean individual size in different populations of the same species would tend to support the view that the evident changes could not have resulted from minor, albeit regular, fluctuations since such physical responses take time to come into effect.

Direct micromammalian evidence

Theoretically, direct information from micromammals is available at the individual, population and community levels. At the individual level changes in average size may indicate changes in prevailing climatic conditions. This is because Bergmann's Rule states that within a given species those members living in colder climates will tend to have a greater body mass than those living in warmer climates (Coon 1962: 59). Guilday (1971: 252) points out, however, that this rule is not universal, some forms being unaffected and some exhibiting a negative response. If it is possible to establish how a particular species reacts with respect to this rule, it may be possible to furnish fairly precise information concerning past temperature fluctuations. The possibility also exists of correlating variation in average rainfall with differences in body mass, as was demonstrated in Israel for *Spalax ehrenbergi* by Tchernov (1968). Physiological studies on the moisture and temperature tolerance or requirements of live animals could perhaps provide information on the usefulness of different species as indicators of these phenomena, as well as the actual limits represented. The accumulation of such data would, however, require extensive long-term investigation.

At the population level it is important to ascertain as precisely as possible which aspect of the habitat is responsible for governing distribution. It will largely be this aspect that the population or species may be said to represent for the purposes of interpretation. It is also likely that changes in the density of a species will indicate changes in the parameter with which that species is correlated. Information concerning habitat preferences of individual species largely comprises general field observations by various collectors. The data provided generally give an indication of plant life-form and state of ground-surface preferred by the species in question, as well as some basic information on food preferences and activity patterns. Detailed distributional data such as those of Lynch (1975) for the Orange Free State are very useful in that they itemize the constituent parts of the habitats in which different species occur. All such information, however, suffers the major disadvantage of being purely descriptive. What is needed is a quantitative assessment of the relative importance of different elements of the habitat in determining the distribution of

individual species. In this respect the work of Rosenzweig & Winakur (1969) is of great theoretical importance, and that of Bond *et al.* (1980) on local species is of direct relevance. These studies consider the factors governing distribution of different species. In both cases the conclusion is that plant life-form and foliage density exert major influences on small mammal distribution, and in a variety of ways as is discussed by Saint Girons (1977). Plant species diversity, on the other hand, appears not to be of great importance. This would appear to confirm the statement by Schulz (1953, quoted by Davis 1973) that density and nature of cover are far more important than the plant species involved. The fact that plant life-form is apparently so important it would suggest, in fact, that even available general ecological information may allow some acceptable interpretation of past vegetation changes. It is important, however, to note that micro-mammalian evidence cannot now, and probably never will, provide information concerning the floristics of a given area.

Qualities of ground surface were also assessed for their role in determining species distribution. Rosenzweig & Winakur (1969) concluded that these abiotic variables were of secondary importance. Bond *et al.* (1980), on the other hand, showed that specific size and abundance of stones or rocks were important habitat components for *Aethomys namaquensis* and *Acomys subspinosus*, although in the former case the correlation might have been fortuitous. Nel & Rautenbach (1975) found that the structure of the substrate restricted distribution of burrowing species. In so far as the nature of the substrate and the amount of rainfall affect vegetation, these factors may also be said to influence the distribution of species reliant on type of vegetation cover.

Changes in population density will appear as changes in community composition in the subfossil evidence. This is because this evidence is such that it shows only the relative abundance of the constituent populations of the small mammal community. It would be difficult, if not impossible, to demonstrate absolute change in individual mean population density because the relationship of the sample to the living population is not known. In fact, it is likely that changes would have the effect of changing community structure whether they resulted from the simultaneous independent reaction of individual populations or from interrelated reaction. It may be possible, and it is certainly desirable, to distinguish the two types of reaction. The latter, for example, may appear as an inconsistency in the evidence and, as such, should be recognizable and explainable. Such a situation, which could be due to interspecific competition, may be illustrated by the relationship of *Otomys irroratus* and *Rhabdomys pumilio*. Both have a preference for dense vegetation, but *R. pumilio* has wider tolerance. Brooks (1974) concluded that when there is competition in the area of overlap the narrow-niche species, *O. irroratus*, has the advantage over the broad-niche species, *R. pumilio*, because of greater specialization. *R. pumilio* would then be forced to make use of less suitable habitats where, presumably, its density would be reduced. In this situation the increase in *O. irroratus* and decrease in *R. pumilio* would be interdependent and apparently contradictory.

An independent parallel response is suggested by the decrease in *O. irroratus* and increase in *Aethomys namaquensis* which would result from reduction in plant cover and change to more arid vegetation. Work such as that of Neal (1970), Sheppe & Osborne (1971), and Nel & Rautenbach (1975) shows habitat utilization in operation at the community level. This suggests that it should be possible to establish a correlation between community composition and a known set of conditions. Thereafter, if the relationship of the various species can be determined, it may be possible to postulate the manner in which the set of conditions must have been different to support a differently composed community.

Predator-related factors

An ideal sample will represent exactly the size and composition of the living population from which it is taken. However, as Simpson *et al.* (1960: 110) have pointed out, perfect sampling is an impossible ideal which not even the most rigorous collecting methods will achieve. In the present case, the sample does not approach the ideal because the method of its acquisition prevents this. It is necessary to attempt to determine the manner and extent of its deviation from the ideal. The extent to which the collecting habits of the predator may have biased the sample must be investigated. *Tyto alba* (barn owl), which is assumed to have been the predator responsible, has been shown to be an effective sampler of small mammal populations in that it preys on most, if not all, of the species to be found within its hunting territory (Vernon 1972; Dean 1977). On the other hand, it has also been shown not to take its prey in direct proportion to relative abundance (Glue 1967; Hanney 1963).

It must be noted at the outset that the methods used to check the relationship of the sample taken by the owl to the structure of the living population in the area hunted, may themselves be subject to bias. Trapping is the most usual method employed since it is the only viable way of controlled sampling. Here the type of trap used can affect the results (Neal & Cock 1969; Wingate & Meester 1977). Moreover, some small mammals are known to be trap-shy and some will not take bait (Hanney 1963; Davis 1973). All these factors may operate to bias the sample, although, being aware of the problems, workers generally take steps to reduce their possible effect. There remains, however, the problem of the extent to which trapping results may be directly comparable with those obtained from owl pellets. Glue (1967), for instance, points out that the owl sometimes hunted outside the area trapped and that this fact could, to some degree, influence the validity of the comparison. Hanney (1963), on the other hand, suggests that direct comparison of his results is precluded by the fact that the pellets were accumulated over bi-monthly periods, whereas the trapping was carried out at the end of each such period. The pellets thus constituted an average for the period, whilst the trapping represented the situation only at the end of the period. In view of seasonal variation this could well affect the comparison of the two sets of data. The

composition of prey-remains of other birds of prey or carnivores which hunt in or near the territory of *T. alba* may provide some confirmation of the data. In general, however, it is to be expected that too many variables will be operating to make comparison useful for assessing biases inherent in the *T. alba* sample.

The effectiveness of *T. alba* as a small mammal sampler is indicated by the fact that Vernon (1972) found four more species in owl pellets from the S.A. Lombard Nature Reserve than did Meester (1955) by trapping. Coetzee (1963) encountered a similar situation in the Kruger National Park. Glue (1967) and Dean (1977) have also shown that *T. alba* takes a far wider range of prey than do other raptors with which it was compared. In this context it is interesting to note that Honer (1963) found that *T. alba* in the Netherlands displayed a preference for hunting-territories that showed a range of elevation. In such situations there would presumably be more niches available and, therefore, a greater variety of small mammal species. The number of pellets it will be necessary to analyse will depend upon the complexity of the community on which the owl is preying. In some areas where few species occur, a small collection will suffice. In other areas such as the Congo valley which has a very rich small-mammal fauna, a large collection will be necessary. This is shown by the fact that out of a total of 2 126 individuals from pellets and bulk samples, only two each of *Dasymys incomtus* (shaggy swamp-rat) and *Steatomys krebsi* (Cape fat mouse) have been recovered (see Table 7). Moreover, the only specimen of *Crocidura flavescens* (red musk-shrew) from Nooitgedacht A was recovered from pellet no. 343. The presence of what one might term trace elements does, however, suggest that over a period of time virtually all the species occurring in an area will be sampled by *T. alba*.

There are, of course, physical limits to the size of prey which the owl will be capable of taking, so that only that part of the mammal community within a certain size range will be sampled. The limits of prey taken by *T. alba* have been discussed above but it is important to note that these limits include all the Insectivora and virtually all the Rodentia that are likely to be found in the southern Cape. Within the limits, however, there is the possibility of a bias in favour of animals at the larger end of the scale. This is because, as Sparks & Soper (1972: 76) have pointed out, all things being equal, it would be more economical in terms of the bird's energy budget for the owl to catch the larger animals. If, therefore, a relatively small species is a particularly abundant prey item, it would appear either that sparse cover and/or an abundant population make capture easy or that very small numbers of larger prey species are available. In this case, a deviation from what may be regarded as the norm could prove significant for the purposes of interpretation.

A second bias is introduced by the obvious need for coincidence in activity patterns in the predator and the prey, a point also made by Davis (1958) and Brooks (1974). Those species which are diurnal are clearly less likely to be preyed upon by *T. alba*, which is nocturnal. In this context Dean (1977) recorded a higher proportion of diurnal *Rhabdomys pumilio* (striped field-

mouse) in pellets of *Asio capensis* (marsh-owl), which hunts during the day, than in pellets of *T. alba*. Brooks (1974) recorded a similar situation. It therefore follows that there is likely to be an unnaturally low proportion of diurnal species in a sample collected by *T. alba*. This, however, is unlikely to cause a major imbalance in the results because the majority of the insectivores and small rodents is nocturnal, crepuscular or active night and day. Apart from *R. pumilio*, only the Macroscelididae (elephant-shrews) are said to be diurnal (Roberts 1951: 26).

There is also some evidence to suggest that *T. alba* is selective in its choice of major prey item. Glue (1967) analysed pellet contents from a site in England and undertook a trapping-programme in the area hunted by the owls. This showed that almost twice the proportion of *Microtus agrestis* (short-tailed vole) (79% as opposed to 40%) was found in the pellets as in the traps. Conversely, *Rattus norvegicus* (brown rat) and *Arvicola terrestris* (water-vole), which were shown to be present in reasonable numbers, seldom occurred in the pellets. Glue (1967: 178) concluded that the owl either preferred *M. agrestis* or found it easier to catch, even though the two sets of data may not be directly comparable, as was discussed above. Hanney (1963) found a similar lack of correlation between trap results and pellet contents. Although *Praomys natalensis* (multi-mammate mouse) was dominant in both, proportions were generally very much higher in the pellets, which suggests concentration on this species out of proportion to its relative abundance on the ground. From this it would appear that, although its actual numerical importance may be exaggerated, the species favoured by the owl will tend to be numerically dominant on the ground. This seems reasonable in view of the fact that such a species must normally be more at risk than a rare species. Indeed, Craighead & Craighead (1956: 364) maintain that prey density is of primary importance in determining on what raptors will feed. Furthermore, they are of the opinion (Craighead & Craighead 1956: 138) that, in general, the diet of the raptor will reflect prey densities of those species available within the habitat of the predator and vulnerable to it.

In some cases a relationship has been noticed in changing proportions of major prey items. This not only illustrates the types of reaction discussed above, but adds the further possibility of the introduction of predator bias. Craighead & Craighead (1956: 182) make the general point that as density or vulnerability of the major prey item declines, other species will be taken to a greater extent by raptors capable of taking them. An example is given by Hanney (1963), who noted that there was a tendency for numbers of *Crocidura* sp. (musk-shrew), the secondary prey item, to vary inversely in relation to those of *P. natalensis*, the major prey item. Whether increases in numbers of *Crocidura* sp. in pellets reflect increases in actual numbers or whether they were an artefact of reduced numbers of *Praomys natalensis*, is not known. Two further examples suggest that both situations are possible. Dean (1977) noted that in *T. alba* pellets proportions of *P. natalensis* declined over a three-year

period while proportions of *Otomys angoniensis* (Angoni vlei-rat) rose: In this case the fact that the same shift in emphasis was observed in the prey remains of *Tyto capensis* (grass-owl) and *Asio capensis* (marsh-owl) may suggest that there was a real switch in the numerical importance of the two species. Glue (1967), on the other hand, found that when the number of *Microtus agrestis* declined, the owls turned their attention to *Rattus norvegicus*, a species which previously they had all but ignored. There was, however, no indication of a real increase in numbers of *R. norvegicus* (Glue 1967: 180), so that the increase apparent in the pellets was due solely to a reduction in the major prey item. It is unfortunate that it probably would not be possible to detect such a situation from the subfossil material. It is perhaps, therefore, more correct to speak in terms of an increase in relative importance of a particular species, and hence vegetation type, rather than an absolute increase. This, again, would tend to confirm the suggestion that it is only possible to show changes in relative abundance in the community.

Even though the major prey item remains the same, it has been shown that there may be fluctuations in total prey composition. In England, Glue (1967) has noted that a greater variety of species was taken during the summer, which may be correlated in some way with the fact that this was the breeding-season of the owls. In Malawi, Hanney (1963) found seasonal fluctuations in the proportions of some species which were unrelated to any shortage in supply of the major prey item. In the Transvaal, minor prey items constituted a steady proportion of the total prey but the composition of that minor prey element varied (Dean 1977). Craighead & Craighead (1956: 183) maintain that an increase in the proportion of minor prey items will result from a decline in the vulnerability of the major prey item which, nevertheless, will not itself decline proportionally. Whatever the reason, such fluctuations would appear to have been short-term and, as such, not visible in the subfossil record. It is thought, in general, that the potential contribution of the minor prey elements to the present study will normally be low, and for this reason they have been given little weight.

The size of the hunting-territory regularly frequented by *T. alba* is thought to have a radius of about 5 km (Kowalski 1971: 473), but the distance covered must depend to some extent upon the availability of food. Indeed, Coetzee (1963: 115) quotes Bodenheimer (1949) as saying that the range in Israel is between 5 km² and 25 km², depending upon the availability of prey. Thereafter, the question arises as to how far it is legitimate to generalize from the relatively small area of the owl's hunting-territory to a wider area. It is unlikely that vegetational or climatic conditions will be strictly limited to the area in which the owl hunts, except perhaps in the desert where distribution of vegetation may be definitely circumscribed. This being the case, it is necessary to establish the present extent of what may be termed a homogeneous unit. In order to do so it is first necessary to decide on an acceptable level of generalization. This process may be illustrated by reference to Boomplaas A.

Since the hunting-territory of the owl must encompass several vegetational categories as defined by Moffett & Deacon (1977), such a category must constitute too low a level of generalization. In practice both here and elsewhere, it will probably happen that a topographic division will provide an acceptable unit, with the added advantage that it is unlikely to have changed during the period under discussion. Thus, in this case, the Congo valley may perhaps be taken as representative of the foothills of the Swartberg Mountains, as distinct from both the mountains themselves and the Little Karoo. These are distinct from each other and from the foothills in climate, vegetation and substrate. Byneskranskop, on the other hand, may perhaps reasonably be taken as representative of the south-western Cape coastal foreland. When sites are far apart or in very different situations, comparison must necessarily be on an even more general scale. Provided that this is made clear, such generalities can still provide useful working hypotheses which can be confirmed or refuted when more information becomes available.

METHODS

Investigation of changes in community composition involves computation of minimum numbers of individuals, multivariate statistical analysis of these data and, finally, the interpretation of the analyses. The methods used in each stage are described below. The measurements taken to provide basic data for the examination of different populations and the indices employed to describe community structure are also explained.

COMPUTATION OF MINIMUM NUMBERS

In accordance with general practice in micromammalian studies, only the cranial material was examined, although it is intended at some later date, when time and a comparative collection allow, to attempt to analyse the postcranial material. In order to estimate minimum numbers of individuals, left and right mandibles and maxillae were enumerated separately for each species and the highest number taken. If several stratigraphic units or squares were to be considered as a whole, the total counts for each jaw were first obtained and then the highest number was taken. In the problematic cases of *Myosorex/C. cyanea* and *Dendromus* spp., further calculations were necessary in order to obtain the correct total minimum number of individuals. The minimum number of certainly identified individuals was obtained in the usual way. The minimum number of doubtful specimens was then obtained by subtracting the sum of certainly identified minima from the total minimum number for the combined group. If the answer was negative, no doubtful specimens were required to make up the total. The following examples illustrate the process:

Example 1

L. maxillae: 1 *M. varius* + 1 *C. cyanea* = 2

R. maxillae: 2 *M. varius* + 1 *C. cyanea* = 3

L. mandible: $10 M. varius + 5 C. cyanea + 4 ? = 19$

R. mandible: $6 M. varius + 5 C. cyanea + 3 ? = 14$

Minimum number for total = 19

Minimum number *M. varius* = 10

Minimum number *C. cyanea* = 5

Minimum number ? = 4

Example 2

L. maxillae: $2 M. varius + 1 C. cyanea = 3$

R. maxillae: $1 M. varius + 1 C. cyanea = 2$

L. mandible: $11 M. varius + 3 C. cyanea + 1 ? = 15$

R. mandible: $7 M. varius + 5 C. cyanea + 2 ? = 14$

Minimum number for total = 15

Minimum number *M. varius* = 11

Minimum number *C. cyanea* = 5

Minimum number ? = 0

Higham (1967: 302) and Clason (1972: 141) have pointed out that various methods of obtaining minimum numbers have their disadvantages and may provide different answers. The method used here is considered the most practical for dealing with large samples since a more detailed examination of the material would be too time-consuming. On the other hand, certain precautions were taken in order to standardize counting, with a view to preventing the possibility of raising the numbers artificially. To this end, jaws were counted only if they included a certain frequently preserved element that was determined for each species or group of species. Specimens that did not possess this element were not counted as they could potentially have broken off others that did. Similarly, even though a loose tooth of a rare species might have been noticed, it was not counted because this would have resulted in a lack of consistency and an over-representation of such species. As it is, the method employed will have tended towards a general under-representation. It is felt, however, that a conservative estimate is to be preferred.

MULTIVARIATE STATISTICAL ANALYSIS OF PRIMARY DATA

The quantity of material involved (Tables 1-7) made it difficult to isolate by simple graphic methods alone the underlying patterns which were assumed to exist. For this reason it was considered appropriate to employ some form of multivariate statistical analysis as an aid to interpretation of the evidence. It was decided that factor analysis could prove useful because of its data-reduction capabilities. Its main aim is to simplify the data by explaining as much as possible of the variation present in terms of as few patterns or factors as possible. In effect, each pattern or factor represents a cluster or group of the original variables. Conversely, the meaning of the factor is established by reference to the variables which load highly on it. Both Cattell (1965b: 424) and Rummel (1967: 451) have pointed out that factor analysis can serve a useful function in the exploration of new fields of research by generating hypotheses.

Its simplification of the data allows the identification of patterns not otherwise apparent, and herein lies its advantage in the present work.

Factor analysis is very complicated and, consequently, there may be problems in its application, more particularly since it was designed for a different type of research. As Doran & Hodson (1975: 198) point out, factor analysis was developed for and by psychologists with a different set of problems in mind from those encountered by archaeologists. Whilst they are inclined to doubt its usefulness in archaeology, Cattell (1965a: 192) makes it clear that it has potential in a great many fields. Thus it appears that, although somewhat different, its use in the present situation cannot be ruled out *a priori*. In fact, the problems that arise would seem to be due mainly to inadequacies in the data rather than to the inherent unsuitability of the method. These questions must be considered and evaluated before use of the analysis can be made.

The first question that arises is whether or not the data are suitable for submission to this form of analysis. The use of factor analysis in the present circumstances could be questioned on the grounds that the basic data comprise frequencies; these are ordinal-level measurements (Nie *et al.* 1975), whereas interval- or ratio-level measurements are required for factor analysis. It may be argued, however, that the numbers represent the score of each species for the given level, which would mean that, effectively, they were ratio-level measurements. Whilst the logic of this argument may be doubtful in terms of pure statistics, it is considered to be acceptable for the purposes of the present research. It was, therefore, considered permissible to use factor analysis in these circumstances, the more particularly since it is, in fact, the most appropriate analysis to the problem at hand. At some later stage it may become possible to refine the data base to make it more closely applicable to factor analysis.

The suitability of the samples may also be called into question. Some of the problems concerning excavated samples have been discussed above, but there are some which are directly relevant to the analysis. Rummel (1967: 452) points out that research can centre on describing the data matrix alone, in which case statistical problems such as the type of underlying frequency distribution, sample size and randomness of selection are not and need not be part of the research design. However, although factor analysis may be a mathematical rather than a statistical tool, some statistical considerations are involved in the acquisition of a suitable or reliable matrix of correlation coefficients on which the analysis is based. Moreover, it is important to have the coefficients of variation of the variables as low as possible. Since calculation of both coefficients depends on the standard deviations of the variables, it is clear that some attention must be paid to these.

There are two problems, one concerning the absolute size of the samples submitted to analysis, and one concerning variation in the size of the different samples being compared. In the first case the problem more specifically concerns small samples. Small samples, or rare categories, tend to give spuriously high correlations, a point mentioned by Doran & Hodson (1975:

144). This is because frequent values of 0 mark a departure from the condition of a normal distribution, which is a prerequisite for calculation of accurate correlation coefficients. Similarly, a small mean will tend to have a relatively larger standard deviation, with the result that correlation coefficients will be artificially raised. In order to obviate this problem, small samples were omitted from analysis in the present study and only data for the most highly represented species were used in the analysis. In some cases data for different levels were either omitted or combined, as has been advised by Cowgill (1968: 373). This, however, was done as infrequently as possible because of the loss of information entailed.

Variation in the size of the samples made it difficult to achieve the desired effect of keeping variability in the scores of the variables on the cases as low as possible. In practice it generally happens that when the levels are considered as variables, a small number of species will dominate the fauna while there are others that occur in very small numbers. This will necessarily result in high standard deviations. Similarly, when the species are considered as variables there are also very high standard deviations because of the considerable difference in the amount of material available from the individual levels of a site. If the large standard deviations are caused by obvious outliers it may be advisable to reduce, or increase, these numbers specifically in some way in order to moderate their effect on the analysis. In the present work, because there was such a large amount of material from levels OLP2 and OLP3 at Boomplaas A, the scores of all species on these levels were divided by ten in an attempt to bring these scores within the general range. Similarly, the scores of species on level 5 at Byneskranskop 1 were divided by five, and an experimental analysis for Die Kelders 1 M.S.A. samples was carried out with the scores on levels 1, 2, and 12 to 14 multiplied by ten. More pervasive variability, on the other hand, requires more general treatment for its reduction. In the present study it was decided, after some experimentation, that \log_{10} transformation seemed to provide the best solution. Although there was still considerable variation, it was felt that any further transformation would destroy meaningful variability in the samples. The use of percentages may appear to solve the problem since the sample size is thereby standardized and, consequently, the mean will be the same. However, in the present work this advantage was militated against by the fact that the standard deviations and, therefore, the coefficients of variation, tended to be considerably larger than in the \log_{10} transformation. Moreover, the use of percentages has the effect of increasing negative correlations because as one category increases one or more others must be reduced in compensation. Although Doran & Hodson (1975: 145) mention that this effect is likely to diminish as the number of categories increases, they note that the detailed effects are not known. In conclusion, whilst it is probable that the matrices achieved by \log_{10} transformation are not ideal, from an empirical point of view the output from the analyses appears to be logically interpretable in terms of the research at hand. Moreover, experi-

ments to reduce the standard deviations did not substantially alter the results in most cases.

The analyses were carried out on a Univac 1110 computer at the University of Stellenbosch, using the subprogramme Factor of the *SPSS: statistical package for the social sciences* (Nie *et al.* 1975). There are various options open to the user of this programme which are explained by Kim (1975) and which pertain principally to the method of factoring and the subsequent method of rotation to the final solution. On the advice of R. G. Klein (1975 pers. comm.), the matrices were originally submitted to principal factoring without iteration (PA1) and the resultant principal components were rotated orthogonally by the Varimax method, which centres on simplifying the columns of the factor matrix (Kim 1975: 485). These options have been used with interesting results by Klein (1976, 1977) on macromammalian faunas from Klasies River Mouth and Border Cave. It was subsequently decided, however, to investigate further options. Consequently, the method of factoring was changed to principal factoring with iteration (PA2) and the method of rotation to Oblique. PA2 factoring was suggested by the SPSS manual (Kim 1975) as the most useful general purpose method. Oblique rotation was chosen because, by allowing that the factors may be correlated, it is intrinsically more likely to fit the situation in nature (Cattell 1965*b*). It is also consequently more flexible in achieving the best possible clustering of variables, particularly where moderate or high correlations are shown to exist between factors. This means, in effect, that the higher the correlation between the factors the greater will be the difference between the Oblique and Varimax solutions. Moreover, the Oblique solution provides more detailed information than the Varimax solution. This is because the factor-pattern and factor-structure matrices, which are combined in the Varimax solution, are separate in the Oblique solution. The factor-pattern matrix is of particular importance for the present study because it distinguishes clusters of variables. Thus, not only are the clusters better defined by Oblique rotation, they are also more clearly represented in the factor-pattern matrix. Here the position of the variable in a cluster is indicated by its loading; the higher the loading the more central the variable is to the pattern represented by the factor. The loadings in this matrix more closely correspond to regression coefficients while those in the factor-structure matrix are correlation coefficients as they are in the Varimax solution. The structure matrix does not distinguish clusters of variables and, as such, is not of importance for present purposes. Since Rummel (1967: 467) makes the point that it is permissible very roughly to interpret the loadings of the pattern matrix as correlations, it is possible in general terms to compare the results of the Varimax rotation with the Oblique factor-pattern matrix.

The data which were submitted to analysis consisted of the counts for the microfauna from different levels at several archaeological sites which have been described above. For the purposes of analysis the microfaunas were restricted to the species that were best represented, for the reasons given above. In the

case of the analyses concerning more than one site, they were further restricted to species occurring in adequate numbers at all the sites concerned. Grouping of levels in various sites was kept to a minimum so as not to mask or distort any inherent evidence of change. Basically there are two ways of considering the data. The species may be grouped according to fluctuations from level to level in their contribution to the fauna. The alternative is to group the levels according to the composition of the microfauna of that level. In terms of factor analysis the former constitutes an R-mode analysis and the latter a Q-mode analysis. However, since the programme handled only R-mode analysis, the data matrix had to be transposed manually before it could be analysed. In terms of the research in hand, grouping of the species, that is, having the species as variables, allowed the identification of different environmental patterns. It was possible, for instance, to identify a glacial pattern which involved extensive grass cover among other things. Grouping of the levels, or using the levels as variables, allowed, in effect, the previously established environmental patterns to be assigned to specific periods within the general framework.

For the purposes of interpretation one recognized restriction was accepted. This allows that only solutions containing factors with an eigenvalue of 1 and over were selected for rotation and, therefore, interpretation. Since the eigenvalue is a measure of the relative amount of variance explained by a particular factor, this ensures that only the most important factors are considered. In the present context a high loading is taken as being one of 0,71 and above. This represents 50 per cent and above of the total variance explained since the percentage is the square of the loading. High loadings on the same factor suggest that variables are varying together in a meaningful way (Klein 1981). Moderate loadings are defined as being those from 0,40 to 0,70 inclusive, with low loadings being those below 0,40. These two categories are arbitrary, for use in the general description, and are not claimed to have any mathematical significance.

A series of analyses was performed, first for individual sites and then for various combinations of sites. Individual analyses were performed for the sites with good sequences, namely Boomplaas A, Byneskranskop 1, and Die Kelders 1 M.S.A., in order to establish the internal patterns of variation within the sites. Thereafter, a coastal analysis was performed, including the Byneskranskop 1 and 2 samples as well as the Die Kelders 1 M.S.A. and L.S.A. level-12 samples. Only the level-12 sample from the L.S.A. levels was sufficiently large to be included in the analysis. In effect, grouping these samples from one small area produces artificially a long sequence comparable to that from one site such as Boomplaas A. The chances of locating possible cycles of change are clearly enhanced in a longer sequence so that it is advantageous to create one, where possible, where it does not exist naturally. The purpose of two further analyses was to test the amount of comparable change discernible in contemporary sequences at a distance from each other. Thus, an Upper Pleistocene analysis was performed using samples from the lower half of the Boomplaas A

sequence, the Die Kelders 1 M.S.A. levels, Klasies River Mouth 1A levels 15 and 32, and Nelson Bay Cave levels YSL and YGL. To these were added the modern samples in order to check for comparison with the present situation at the same time. An additional aim of this analysis was to establish whether there was any basis for site correlation through comparison of changing micromammalian composition, since radiometric dates are not available for much of the material. Finally, a Holocene analysis was conducted using the Byneskranskop 1 material and that from the contemporary levels at Boomplaas A. Again the modern samples were included, for the same reason as before. In all cases where analyses of multiple samples were conducted, the data base was restricted to those species that occurred in adequate quantities at all sites involved. It was hoped in this way to remove local factors from the comparison. In the case of the coastal analysis, a check was effected by running the analysis with and without *Steatomys krebsi*, a species present in large numbers in the Holocene but absent from the Upper Pleistocene. It was discovered that, although constituting the most obvious difference, it was by no means the sole distinguishing feature. In general, however, it was felt that it was preferable merely to omit such species.

PROCESSES FOR INTERPRETING ANALYSES

Interpretation of analyses comprises three parts. The first of these entails the establishment of the common denominator of the variables (species or levels) loading highly on each factor. In the case of the species, this will be the pattern of changing proportions of the individual species in the community. Thus, species occurring in greater numbers in the Upper Pleistocene will load on a different factor from those occurring in greater numbers during the Holocene. The first factor will, therefore, represent Upper Pleistocene conditions and the second Holocene conditions. In the levels analyses, the situation will be reversed and levels with similar faunal composition will be grouped together. Thus different factors will be characterized by high, or low, proportions of particular species.

The second stage in the procedure is to interpret the meaning of the factors. In the species analyses, this will entail translating the species that load highly on each factor into their environmental equivalent. Thus, having established that a factor represents Upper Pleistocene conditions, one can then proceed to suggest what those conditions comprised. The levels analyses provide, in effect, a cross-check for the interpretations, since the same picture is being viewed from a different angle. The two types of analysis are also complementary; it is possible to establish both which element (species = environmental equivalent) is most important during a given period and also more precisely when during that period conditions thus indicated would have pertained in their purest form. Naturally, interpreting only the variables that load highly will provide only a partial interpretation of the meaning of the factors. This will, however, establish the general patterns, which is the aim at this

preliminary stage. Certainly Klein (1976) has produced eminently worthwhile results in this manner and it is doubtful whether there is sufficient information currently available to make an attempt at a more detailed interpretation appropriate at this time.

The final stage in the interpretation involves employing the information acquired thus far to construct a history of past environmental change. To this end, the species analyses, together with the visual aids (Figs 8–12), are used to show the general trends of climatic and vegetational change. The levels analyses, together with the relevant visual aids (Figs 9–13), delineate and characterize periods of similar climate and vegetation. Beyond this, lesser fluctuations within periods can be ascertained by examining changes in the faunal composition in the different levels.

MENSURATION AND CALCULATION OF INDICES

Variation in mean individual size and in species diversity was investigated. Calculations concerning the former were all based on a series of measurements taken from individual specimens. These measurements had, for the most part, to be determined by the part of the specimen that was most frequently preserved. For this reason the measurements might not have been those most likely to reflect change in the overall mass, although, taken together, they may perhaps be indicative of such changes. Differences between populations, as well as any possible trends, were examined in order to establish the potential of this line of investigation. Changes in the patterns of community structure were also examined in order to establish whether or not there was any correlation with known climatic changes. General diversity, which includes both species richness and species equitability, provides a basic pattern. Splitting of the general index into its component parts should give some indication as to which is the more important element.

Mean individual size

Measurements were taken on mandibles and/or maxillae of individuals belonging to five species. Of these *Crocidura flavescens* and *Myosorex varius* were chosen because the former shows some indication of a positive reaction to Bergmann's Rule, while the latter may well exhibit a negative response (J. Meester 1978 pers. comm.). It was anticipated, therefore, that these species might provide some evidence of temperature changes in the past. *Cryptomys hottentotus* was chosen because it is known to vary in size through its present range (De Graaff 1981) and because *Spalax ehrenbergi*, which is also a mole-rat, is known to vary in size in Israel according to the annual rainfall (Tchernov 1968). *Tatera afra* and *Aethomys namaquensis* provided some adequate samples for measuring and were therefore examined without any prior expectations. All measurements, which were taken with Helios needlepoint dial calipers, were expressed in millimetres and calculated to the first decimal place.

In *Crocidura flavescens* up to five mandibular measurements were taken where possible. These are as follows:

- A. height of ascending ramus, being the distance between the superior and inferior surfaces of the ascending ramus, measured perpendicular to the line of the jaw (see Fig. 7);
- B. depth of mandible, being the distance between the superior and inferior borders of the body of the mandible, measured between M_1 and M_2 in the lingual aspect and perpendicular to the line of the jaw;
- C. length of M_{1-3} , being the distance from the posterior surface of M_3 to the anterior surface of M_1 , measured along the line of the jaw;
- D. length of the lower tooth row (L.T.R.), being the distance from the posterior surface of M_3 to the tip of I_2 , measured along the line of the jaw;
- E. length of mandible plus incisor (M+I), being the distance from the most posterior point of the articular condyle of the lower jaw to the tip of I_2 , measured along the line of the jaw (see Fig. 7).

Parameters D and E were included because they are standard measurements (Meester 1963:5). However, because these parameters could be taken too infrequently to allow reliable statistical comparisons to be made, parameter C was taken as an alternative measurement. Parameters A and B were taken because it was thought that they might give an indication of shape, either alone or in conjunction with a length measurement. Tchernov (1968) used depth of mandible for this purpose.

In *Myosorex varius* four measurements were taken where possible. These are as follows:

- A. height of ascending ramus, as in *Crocidura flavescens*;
- B. length of mandible plus incisor (M+I), as in *C. flavescens*;
- C. length of lower tooth row (L.T.R.), as in *C. flavescens*;
- D. length of P_4 to M_3 , being the distance from the posterior surface of M_3 to the anterior surface of P_4 , measured along the line of the jaw.

For *Cryptomys hottentotus* five measurements were taken, where possible, on the mandible. These are adaptations of the measurements taken by Tchernov (1968) on *Spalax ehrenbergi* and represent an attempt to provide data for estimating size. The parameters are as follows:

- A. alveolar length, being the distance between the posterior border of the alveolus of M_3 and the anterior border of the alveolus of P_4 , measured along the alveolar row;
- B. M_3 to symphysis, being the distance between the posterior border of the alveolus of M_3 and the posterior border of the symphysis;
- C. maximum depth of attachment of the ascending ramus, being the distance between the superior and inferior borders of the ascending ramus where it attaches to the body of the mandible in the region of M_2 , measured perpendicular to the line of the jaw;

- D. foramen mentale to alveolar margin, being the distance between the foramen mentale and the superior border of the body of the mandible at P_4 ;
- E. depth of mandible, being the distance between the superior and inferior borders of the body of the mandible at M_1 , measured perpendicular to the line of the jaw in the lingual aspect.

In *Tatera afra* it proved possible to measure only teeth. Here the lengths of M_1 , M_{1-2} , M^1 and M^{1-2} were taken. In each case the distance was measured from the posterior to the anterior surfaces of the teeth in question, measured along the line of the tooth row.

For *Aethomys namaquensis* the lengths of M_{1-3} , M_{1-2} , M^{1-3} and M^{1-2} were measured, using the same definitions as for *T. afra*. In addition, the depth of the mandible was also measured, using the same definitions as those given for *C. flavescens*.

In all cases the arithmetic mean (\bar{X}), standard deviation (s) and 95 per cent confidence interval for the mean were calculated as a basis for estimating differences between populations. The coefficient of variability, which is given as $V = \frac{100s}{\bar{X}}$ by Simpson *et al.* (1960: 90), was calculated for selected samples. In the present case the coefficient was used in order to discover which measurements were most homogeneous and, therefore, potentially most useful in distinguishing populations. This is because parameters that exhibit little internal variation should be more effective in distinguishing differences between populations than those parameters that exhibit greater internal variation. Student's 't' test was used to establish whether or not differences between populations were statistically significant. Such significant differences may indicate periods of accelerated change if a short time elapsed between the accumulation of the two samples. Over a longer period of time the indication would be of the extent of the change involved.

Patterns of community structure

The Shannon index of general diversity, as given by Odum (1971: 144), was employed to establish the basic character of the communities represented by the samples from the different levels in archaeological sites and from modern owl roosts. This index is calculated from the equation $\bar{H} = -\sum P_i \log P_i$ where $P_i = n_i/N$ = importance probability for each species. The base of the logarithm is immaterial but in the present work natural logarithms (\log_e) were used. As was mentioned above, this index takes into account both aspects of diversity, namely species richness and evenness of importance of each species. Odum (1971: 149) points out that this index is very useful for making comparisons because it is reasonably independent of sample size, which means, in effect, that fewer samples are needed to obtain a reliable index. In the present case this is a definite recommendation because sample size varies quite considerably and some samples are not very large.

It may, however, be useful to distinguish which element of diversity is the more important, especially in an exploratory exercise. Either the number of species or the evenness of representation of the species may be varying. The first index of species richness given by Odum (1971: 144) was employed. In this index $d = \frac{S-1}{\log N}$ where S = number of species, N = number of individuals. The index of evenness is $e = \frac{\bar{H}}{\log S}$ which is, in effect, the converse of the index of dominance $c = \Sigma(ni/N)^2$, where the symbols are as given above. In practice it may not be necessary to distinguish the two components since there is a tendency towards both greater species richness (Krebs 1972: 509) and equitability (Odum 1971: 144) in the tropics relative to temperate and polar regions. This would suggest, in the present context, that a change in either may indicate a response to changing climate. Equally, it may suggest that both parameters will tend to co-vary. On the other hand, Odum (1971: 145) notes that dominance is concentrated in fewer species where physical conditions are extreme. This suggests that dominance may prove an independently useful index of environmental change.

THE MODERN DATA

The basic assumption of palaeoecology is that the ecology of the fossils may be inferred from what is known about equivalent or related living species (Odum 1971: 159). It cannot be otherwise or it would be impossible to proceed. In the present case the propriety of basing research on this assumption is reinforced by the fact that all the species concerned are extant. It follows that it is first necessary to establish as precisely as possible the factors governing distribution and relative abundance of the individual species. In the first instance their ecological distribution will indicate the conditions which they favour and of which they may be said to be indicative. Generally speaking, it would seem that small mammal distribution is influenced by vegetation type. Correlation with other factors is likely to be coincidental, except in so far as those factors will probably be affecting the vegetation upon which the animals are dependent. The principal exception will be the influence which the nature of the substrate will exert on the distribution of burrowing species (Bigalke 1978: 1005).

Proportions of species in the modern samples may be correlated with suitable habitat present in the expected area of the owl's hunting territory. This should provide some basis for comparison of the samples with those from archaeological sites.

ECOLOGICAL DISTRIBUTION

The available information concerning the ecological distribution of the individual species forms the basis for interpretation in the present study. Data regarding the factors that apparently influence distribution have been assembled from the literature and are given below. The species are listed in taxonomic order (see Table 8).

TABLE 8

Taxonomic list of species encountered, together with their English common names.

Order	Family	Genus, species	English common name
INSECTIVORA	Chrysochloridae	<i>Chrysochloris asiatica</i>	Cape golden mole
		<i>Chlorotalpa duthiae</i>	Duthie's golden mole
		<i>Amblysomus hottentotus</i>	Hottentot golden mole
	Macroscelididae	<i>Elephantulus edwardi</i>	Cape elephant-shrew
	Soricidae	<i>Myosorex varius</i>	forest-shrew
		<i>Suncus varilla</i>	dwarf-shrew
		<i>Crocidura cyanea</i>	reddish-grey musk-shrew
		<i>Crocidura flavescens</i>	red musk-shrew
		<i>Crocidura</i> sp.	musk-shrew
	Nycteridae	<i>Nycteris thebaica</i>	Egyptian slit-faced bat
CHIROPTERA	Rhinolophidae	<i>Rhinolophus clivus</i>	Geoffroy's horseshoe-bat
		<i>Rhinolophus capensis</i>	Cape horseshoe-bat
	Vespertilionidae	<i>Myotis lesueuri</i>	Lesueur's wing-gland bat
		<i>Myotis tricolor</i>	Cape hairy bat
		<i>Eptesicus hottentotus</i>	long-tailed house-bat
		<i>Eptesicus capensis</i>	Cape serotine
		<i>Miniopterus schreibersi</i>	Schreiber's long-fingered bat
RODENTIA	Bathyergidae	<i>Cryptomys hottentotus</i>	common mole-rat
	Muridae	<i>Georchus capensis</i>	Cape mole-rat
		<i>Acomys subspinosus</i>	Cape spiny mouse
		<i>Aethomys namaquensis</i>	Namaqua rock-rat
		<i>Dasyms incomtus</i>	shaggy swamp-rat
		<i>Mus minutoides</i>	dwarf mouse
		<i>Praomys natalensis</i>	multimammate mouse
		<i>Praomys verreauxi</i>	Verreaux's mouse
		<i>Rattus rattus</i>	black rat
		<i>Rhabdomys pumilio</i>	striped field-mouse
		<i>Mystromys albicaudatus</i>	white-tailed rat
	Cricetidae	<i>Tatera afra</i>	Cape gerbil
		<i>Gerbillurus paeba</i>	South African pygmy gerbil
		<i>Dendromus melanotis</i>	grey pygmy climbing mouse
		<i>Dendromus mesomelas</i>	chestnut climbing mouse
		<i>Steatomys krebsi</i>	fat mouse
		<i>Saccostomus campestris</i>	pouched mouse
		<i>Otomys laminatus</i>	lamineate vlei-rat
		<i>Otomys saundersae</i>	Saunders' vlei-rat
		<i>Otomys irroratus</i>	vlei-rat
	Muscardinidae	<i>Otomys unisulcatus</i>	bush Karoo rat
		<i>Graphiurus ocularis</i>	Cape dormouse

Nomenclature according to Meester & Setzer (1971).

Insectivora

Chrysochloris asiatica lives in cultivated and uncultivated ground (Shortridge 1942: 32). It occurs not only in sandy soil under Karoo scrub (Shortridge 1942: 32; Rautenbach 1971: 138), but also in alluvial soil under open grasslands (Shortridge 1942: 75).

Chlorotalpa spp. are burrowing species generally to be found in sheltered mountain valleys or forests where they can burrow in the peaty soil (Roberts 1951: 108). Pienaar (1964: 16) notes, however, that they occur in sandy soil.

C. sclateri occurs in areas which experience severe frost and with an annual rainfall of 700 mm (Lynch 1975: 137).

Amblysomus hottentotus burrows extensively in soft but not necessarily sandy soil, generally in open ground with plenty of grass cover (Roberts 1951: 189).

Elephantulus edwardi appears to favour rocky outcrops on grassland (Corbet & Hanks 1968: 97), although Roberts (1951: 29) quotes A. Smith as saying that the type came from 'a locality bearing little or no vegetation, except a few dwarf shrubs'.

Myosorex varius frequents dense undergrowth near streams or swamp vegetation (Shortridge 1934: 37; 1942: 35) in a fairly moist and often montane environment (Brain & Meester 1964: 337) and is often to be found under fallen trees (Thomas & Schwann 1905a: 131, 264). It is also to be found on grassy slopes (Rautenbach 1976: 134). Although it usually exists in wetter areas, it can be found in drier places where dense vegetation or frequent mists presumably counteract the lack of precipitation (Meester 1958: 327). It was found in a wide variety of habitats by Bond *et al.* (1980: 41).

Suncus varilla: at least one subspecies is said to inhabit deserted termite mounds (Roberts 1951: 44).

Crocidura cyanea: the two subspecies are almost entirely restricted to the above and below 500 mm rainfall zones; *C. c. infumata* inhabits the former in a wide range of vegetation while *C. c. cyanea* occupies the latter in steppe and fynbos vegetation (Meester 1963: 54, 58). Shortridge (1942: 53, 78) records the fact that *C. c. cyanea* favours rocky, stony country while Rautenbach (1976: 135) notes that what is presumably *C. c. infumata* occurs in dense grass along a stream-edge.

Crocidura flavescens is generally stated to prefer dense undergrowth (Thomas & Schwann 1905a: 130), normally in rocky or broken country (Meester 1962: 77; Sclater 1900-1: 162). It also occurs in and around cultivated land (Thomas & Schwann 1905b: 264). At one time it was thought to be restricted to the above 750 mm rainfall zone (Meester 1963: 39) but it now seems that it is able to survive in drier areas where there is sufficient ground cover or mists (Swanepoel 1975: 118). It does not seem to be restricted to any particular type of vegetation (Meester 1963: 77).

Rodentia

Cryptomys hottentotus is a burrowing species which occurs both on mountain plateaux and in low-lying areas (Shortridge 1942: 97; Rautenbach 1976: 136), where it may be found on and between dunes (De Graaff & Nel 1970: 180; Rautenbach 1971: 141). It seems to avoid severe frost conditions (Lynch 1975: 137). It apparently prefers more open grassy vegetation, but is also found in fynbos (Stuart n.d.).

Georchus capensis burrows extensively in sandy or other loose soil, whether cultivated or not, usually in areas bordering pans and the like (Roberts 1951: 382; Sclater 1900-1: 76).

Acomys subspinosus is generally said to prefer rocky situations (Roberts 1951: 465; Davis 1962: 62), and Bond *et al.* (1980) correlated its occurrence with rocks 1 m in diameter. Shortridge (1942: 92) further noted that it occurred on heathy slopes and plateaux. Bond *et al.* (1980: 39) found that it favoured high-altitude areas with dense phytomass, especially below 60 cm. On the coast it appears attached to thick undergrowth at the edge of forest (Thomas & Schwann 1906a: 164) and to forests and woodlands (Andrews *et al.* 1975: 24).

Aethomys namaquensis is generally described as frequenting rocky hillsides (Sclater 1900–1: 43; Roberts 1951: 482). Bond *et al.* (1980: 40) have found its distribution strongly correlated with the occurrence of stones up to 13 cm in diameter, but have suggested that this may be fortuitous. It is sometimes to be found in flatter areas (Shortridge 1934: 295; De Graaff 1974: 178). Although this is usually in areas where there are rocks (Thomas & Schwann 1904: 179), it has been recorded from river-banks and even dune areas (Rautenbach & Nel 1975: 197). It appears to prefer scrub (Hanney 1965: 596; Bond *et al.* 1980), but Ansell (1960: 92) records it as living in woodland. Stuart (n.d.) also noted that, although it occurred in indigenous forest, it preferred short to medium fynbos at higher altitudes. Bond *et al.* (1980: 40) have found its occurrence correlated with sparse (less than 75 per cent total shrub cover) succulents. It was also restricted to areas of less than 10 per cent microphyllous shrubs.

Dasymys incomtus is generally stated to inhabit dense vegetation on the banks of streams, edges of swamps, reed-beds and the like (Roberts 1951: 494; Ansell 1960: 97). Thomas & Schwann (1905b: 270) state, however, that it is not necessarily found close to water and Hanney (1965: 617) found it up to 1 km from streams at high altitudes but within 20 m of water at low altitudes. It is commonly found in grasslands (Pienaar 1964: 22; Davis 1974: 152), and Davis (1962: 62) further states that it is typical of savanna and montane savanna.

Mus minutoides is found in all manner of habitats from dunefields (Rautenbach & Nel 1975: 197) to woodland (Vesey-Fitzgerald 1964: 67) and even forest (Delaney & Neal 1966: 331), on hillsides and on the flat (Thomas & Schwann 1905a: 136). Vesey-Fitzgerald (1966: 117) notes that it occurs where vegetation is usually in decline or secondary.

Praomys natalensis inhabits a diversity of environments including forest, grassland and rocks (Vesey-Fitzgerald 1966: 115), and also cultivated land and houses (Delaney & Neal 1966: 326; Pienaar 1964: 22). It appears, however, to avoid extremes such as desert or semi-desert (De Meneses Cabral 1966: 194; Coetzee 1975: 637) and rain forest (Hubbard 1972: 436). It perhaps has a preference for grassland (Sheppe 1973: 173; Andrews *et al.* 1975: 24) and seems to prefer the vicinity of water (Shortridge 1934: 301).

Praomys verreauxi is said to live among the scrub and bush on rocky hillsides (Roberts 1951: 470; Shortridge 1942: 93) and also in the forest (Roberts 1951: 470; Thomas & Schwann 1906a: 164). There is some doubt as to whether it ventures onto the plains, Shortridge (1942: 93) maintaining that it does not and Thomas & Schwann (1906a: 164) stating that it is found in swamps

and grass-filled hollows in open country. Bond *et al.* (1980: 41) found this species only at mid and high altitudes.

Rhabdomys pumilio is generally stated to prefer dense vegetation, often on stream banks or in dry river-beds (Roberts 1951: 497; Shortridge 1934: 278), even in otherwise very dry areas such as the Namib Desert (Coetzee 1969: 30). The type of vegetation is obviously less important than the amount of cover afforded to this diurnal species since it is found in scrub (Nel & Pretorius 1971: 107), bracken (Hanney 1965: 606), in cultivated land (Shortridge 1942: 607) and even in the Tsitsikama Forest (Smuts 1832: 37), but it may perhaps have a preference for grassland (Smithers 1971: 292; Vesey-Fitzgerald 1964: 66). Bond *et al.* (1980: 38) found that its presence was correlated with continuous or extensive 'grass' patches, 'grass' including Poaceae, Cyperaceae and Restionaceae as well as Gramineae for the purposes of their classification. Brooks (1974) found that it may prefer grassland and vlei at different times of the year, or that it may be forced into less favourable areas by a periodic abundance of a narrow-niche species such as *Otomys irroratus*. Although it seems to have a preference for damp areas (Hanney 1965: 606) which afford immunity from the effects of fire (Vesey-Fitzgerald 1966: 117), it is apparently not restricted to them (Rautenbach 1971: 141).

Mystromys albicaudatus appears to be restricted to grassland, including high-altitude montane grassland where it is an indicator of the transition from savanna grasslands to woodlands (Davis 1962: 64). Roberts (1951: 436) records that it was found in meadowland along a river bank.

Tatera afra prefers to burrow in sandy coastal plains (Shortridge 1942: 89). It is to be found in open ground with short grass (Sclater 1900-1: 21), under bushes and in cultivated land (Roberts 1951: 409).

Gerbillurus paeba lives in sandy areas where the vegetation cover is not dense, in desert and semi-desert areas (Shortridge 1942: 53; Coetzee 1969: 29).

Dendromus melanotis is generally said to live in grassland, whether near trees or not (Shortridge 1942: 91; Davis 1962: 63), both near swampy country and in dry areas (Smithers 1971: 319).

Dendromus mesomelas appears, in contrast to the previous species, to be found more frequently in bush or woodland (Davis 1962: 63; Smithers 1971: 613). However, it also occurs in tall grass and scrub (Ansell & Ansell 1973: 61) and Shortridge (1934: 243) states that it favours damp grass, although it is seldom far from trees and bushes. Kingdon (1974: 532) states that although it has a preference for wet habitats, it will occupy the driest most terrestrial habitat when in competition with other species of *Dendromus*.

Steatomys krebsi apparently lives in more or less open subcoastal grassland and bush (Shortridge 1942: 91).

Saccostomus campestris is generally said to inhabit woodland (Pienaar 1964: 23; Delaney 1972: 11) or at least grassland with scattered trees and shrubs (Sheppe 1973: 184), but not open grassland, at least not in South Africa (Davis 1962: 63). De Graaff (1981) notes wide tolerance in this species. It is also

attracted to cultivated land (Vesey-Fitzgerald 1964: 67; Delaney & Neal 1966: 337). It seems to favour drier country (Hanney 1965: 613; Delaney & Neal 1966: 337), but within reach of water (Shortridge 1942: 59; Thomas & Schwann 1905*b*: 269). It seems to avoid areas of severe frost (Lynch 1975: 137).

Otomys laminatus is recorded from moist submontane and coastal savanna (Davis 1962: 63; 1974: 152), while Thomas & Schwann (1905*b*: 268) state that it occurs among rocks on hillsides and cliffs.

Otomys saundersae is said to share a preference for high altitude and montane grasslands with *O. irroratus* and *O. sloggetti* (Davis 1962: 64), while it is recorded by Shortridge (1942: 89) as inhabiting belts of dry rushes in heathy country on high mountain slopes. According to J. U. M. Jarvis (1978 pers. comm.), it prefers rockier situations with more open vegetation than does *O. irroratus*.

Otomys irroratus is generally stated to inhabit dense vegetation on the banks of streams and edges of swamps (Roberts 1951: 420; Delaney 1972: 120). It is, however, sometimes found at some distance from water (Thomas & Schwann 1905*a*: 135; 1905*b*: 266; 1906*b*: 589; Shortridge 1934: 239) and Bond *et al.* (1980: 39) have found it in a range of habitats, none near water. The occurrence of this species was, instead, correlated with the microphyll layer between 1.0 m and 2.5 m and the total microphyll layer, and its presence was apparently restricted to areas with 75+ per cent shrub cover (Bond *et al.* 1980: 40). Davis (1973) confirmed the occurrence of this species in an area of dense basal and canopy cover.

Otomys unisulcatus is generally said to inhabit drier areas among the scrub vegetation of the Karoo, and rocks on the lower slopes of hills and mountains (Roberts 1951: 427; Shortridge 1934: 244). Nel & Pretorius (1971: 107), however, recorded it from riverine scrub and forest.

Graphiurus ocularis is said to be basically a rock dweller, although to some extent it is found in trees (Roberts 1951: 369; Shortridge 1942: 51). It seems to prefer drier areas with Karoo or 'karoid' vegetation (Shortridge 1934: 216).

THE BASIS FOR INTERPRETATION

The data given above require analysing in such a way as to be useful for interpreting environmental conditions. This involves separating data relative to individual factors or aspects of the habitat. For present purposes, data relating to abiotic factors such as horizontal distribution, especially in areas of high relief, and correlation with different ground-surface and substrate types will restrict application of data forthcoming from biotic factors. In practical terms this means that, for instance, the presence of *Aethomys namaquensis* in a sample will suggest scrub, probably semi-arid, which is specifically most likely to be present on the lower slopes of the hills or mountains. Of the biotic factors, the life form and density of the vegetation may be treated separately. It is possible to establish some sort of correlation between annual rainfall and the incidence of various species, based on geographical distribution, which may

have some broad predictive value. Being homoiothermic, small mammals may be expected to exhibit broad temperature tolerance. Moreover, they often exist in microhabitats which are very different from the macrohabitat. For both reasons it is not considered appropriate to attempt to correlate temperature with small mammal distribution.

In the present context, establishment of horizontal distribution largely consists of determining which species occur on hillsides and mountain slopes. The majority of species occurs on flat ground which, depending on the area being studied, may be the coastal foreland, valley floors, or, possibly, mountain plateaux. Of the six species which Bond *et al.* (1980) trapped on the slopes of the Swartberg Mountains, *Aethomys namaquensis* occurred only on the lower slopes while *Acomys subspinosus* and *Praomys verreauxi* were apparently restricted to the higher slopes. *Otomys irroratus*, *Rhabdomys pumilio*, and *Myosorex varius* occurred at all altitudes. *Otomys saundersae* is said to occur on high mountain slopes (Shortridge 1942: 89) but *Otomys laminatus* may be restricted to lower hillsides or, at least, lower elevations (Davis 1962: 63; Thomas & Schwann 1905b: 268). *Otomys unisulcatus* is apparently also restricted to the lowest slopes, as well as the low ground (Shortridge 1934: 244). *Mus minutoides* has been found on rocky hillsides (Thomas & Schwann 1905a: 136) as well as in a wide variety of other situations. In general, species that occur on hill or mountain slopes appear to be those that are to be found on rocky ground (see Table 9). This being the case, a further group of three species may also occur on hillsides, although this has not been specified. *Graphiurus ocularis* is known to be a montane species (J. U. M. Jarvis 1978 pers. comm.) that frequents rocks (Roberts 1951: 369) and presumably, therefore, mountain slopes. *Crocidura flavescens* is apparently restricted to rocky,

TABLE 9

Correlation between distribution of various species and abiotic factors.

A1: upper slopes	A2: lower slopes	A3: unspecified slopes
<i>A. subspinosus</i>	<i>A. namaquensis</i>	<i>M. varius</i>
<i>P. verreauxi</i>	<i>O. laminatus</i>	<i>E. edwardi</i>
<i>O. saundersae</i>	<i>O. unisulcatus</i>	<i>R. pumilio</i>
		<i>O. irroratus</i>
		<i>G. ocularis</i>
B1: rocky ground	B2: loose sand/soil	B3: sandy plains
<i>E. edwardi</i>	<i>C. asiatica</i>	<i>M. minutoides</i>
<i>C. flavescens</i>	<i>Chlorotalpa</i> spp.	<i>S. krebsi</i>
<i>A. subspinosus</i>	<i>A. hottentotus</i>	<i>S. campestris</i>
<i>A. namaquensis</i>	<i>C. hottentotus</i>	
<i>P. verreauxi</i>	<i>G. capensis</i>	
<i>O. laminatus</i>	<i>T. afra</i>	
<i>O. saundersae</i>	<i>G. paeba</i>	
<i>G. ocularis</i>		

TABLE 10

Correlation between distribution of various species and vegetation type and density.

A1: grass	A2: scrub	A3: woodland/forest
<i>A. hottentotus</i>	<i>E. edwardi</i>	<i>Chlorotalpa</i> spp.
<i>M. albicaudatus</i>	<i>G. capensis</i>	
<i>T. afra</i>	<i>A. subspinosus</i>	
<i>D. melanotis</i>	<i>A. namaquensis</i>	
<i>G. paeba</i>	<i>P. verreauxi</i>	
<i>S. krebsi</i>	<i>O. unisulcatus</i>	
<i>O. laminatus</i>	<i>G. ocularis</i>	
B1: dense vegetation	B2: sparse vegetation	
<i>M. varius</i>	<i>C. asiatica</i>	
<i>C. c. infumata</i>	<i>E. edwardi</i>	
<i>C. flavescens</i>	<i>C. hottentotus</i>	
<i>A. subspinosus</i>	<i>G. capensis</i>	
<i>D. incomtus</i>	<i>A. namaquensis</i>	
<i>R. pumilio</i>	<i>G. paeba</i>	
<i>D. melanotis</i>	<i>O. unisulcatus</i>	
<i>O. irroratus</i>	<i>G. ocularis</i>	

mountainous country (Meester 1963: 40), although this may be in valleys; Sclater (1900-1: 162) mentions wooded ravines. *Elephantulus edwardi* exhibits a preference for rocky ground (Shortridge 1942: 29), including high plateaux, but possibly lower hills rather than steep mountain slopes.

Of the vegetation types, grass and in particular 'grass' *sensu* Bond *et al.* (1980) appears to support the greatest number of small mammal species (Table 10). A certain amount of variation is, however, discernible. Some species, such as *Rhabdomys pumilio* and *Dendromus melanotis*, prefer dense grass-cover. Others, such as *Chrysochloris asiatica* and *Gerbillurus paeba*, occur in much more open grass. Indeed, the latter species is known to decline in years when the grass cover is increased by good rains (J. A. J. Nel 1978 pers. comm.), whereas the opposite occurs in *R. pumilio* (Swanepoel 1975: 123). *Mystromys albicaudatus* and *Dendromus mesomelas*, although they are grassland species, indicate the presence of trees or bushes in the vicinity (Davis 1962: 63). With other species, grass is only one of the life forms in which they occur. Of the species occurring in scrub, it would appear that *Aethomys namaquensis* and *Graphiurus ocularis* are found in both fynbos and semi-arid scrub, although perhaps more often in the latter. In this context fynbos is taken to mean mountain fynbos and semi-arid scrub to mean either succulent vegetation with Karoo affinities or arid fynbos. Woodland or forest, probably riverine or valley floor, is indicated by three species, *Chlorotalpa* spp., *Dendromus mesomelas*, and *Saccostomus campestris*. Reed-beds may be suggested by *Dasymys incomtus* and *Otomys irroratus*, although the latter species in particular is not

restricted to such conditions. A remaining group comprises broad-niche species which occur in a variety of vegetation types.

It is possible to find limited correlation between rainfall (Fig. 1C) and the geographical distribution of individual species. The range appears, in the main, to be fairly broad, but some distinction is possible between a proportion of species occurring in drier areas and those to be found in wetter areas (Table 11).

The main environmental factors indicated by the individual species are summarized in Table 12. This information will serve as the basis for interpreting the information forthcoming from both modern and excavated micromammalian samples. In the present context it should be noted that flats are taken as indicating valley floors and mountain plateaux as well as more low lying areas such as the coastal foreland.

INTERPRETATION OF COMPARATIVE SAMPLES

There are two major collections of comparative material from the Congo valley, which are taken together, and two from the coast, at Byneskranskop 2 and Glentyre. Details of the location of the sites and the methods of collection are given above. Chaline (1972: 273) reconstructed the environment of three modern localities in France in order to show that it was possible to obtain an accurate result. Since this point has, therefore, been adequately proved, it is not necessary to repeat the exercise for this purpose. It is, however, useful to carry out similar reconstructions for the present material for two other reasons. The first is that it provides a means of checking the environmental indications that have been assigned to the species. The second is that it may thus be possible to assess whether there has been a change since the end of the subfossil record, about 1 500–2 000 B.P. in the present samples, and the present. In fact, the introduction of agriculture about 300 years ago has caused major, although quite artificial, changes in the vegetation and it may well not be possible to compare the present situation with that pertaining in the past. A further restriction on interpretation is caused by the fact that the precise area hunted by the owl or owls is not known. For this reason it is not possible to make quantitative comparisons between proportions of small mammals and those of the various vegetation types. Such a lack of precision applies equally to the subfossil material. Some indication of general proportions may, however, be warranted.

Byneskranskop 2 (BNK2)

Basically, the area around BNK2 can be divided into hills, plains and riverside. The hills tend to support fynbos, although this may vary from more restioid to more proteoid depending on the substrate. At the base of the limestone ridges and along the river, coastal scrub is found. The difference is that along the river there is a dense under-layer of vegetation, whereas on the lower slopes of the limestone ridges there tends to be little vegetation beneath

TABLE 11

Generalized correlation between distribution of various species and rainfall (based on distribution in the southern and south-western Cape).

Up to 400 mm	Up to 600 mm	200 mm upwards	400 mm upwards
<i>G. paeba</i>	<i>C. asiatica</i>	<i>M. varius</i>	<i>C. duthiae</i>
<i>O. unisulcatus</i>	<i>E. edwardi</i>	<i>M. minutoides</i>	<i>A. hottentotus</i>
	<i>C. c. cyanea</i> (500 mm)	<i>P. verreauxi</i>	<i>C. c. infumata</i> (500 mm)
	<i>A. namaquensis</i>	<i>D. melanotis</i>	<i>C. flavescens</i>
	<i>S. campestris</i> (500 mm)	<i>D. mesomelas</i>	<i>G. capensis</i>
			<i>A. subspinosus</i>
			<i>D. incommutus</i>
			<i>M. albicaudatus</i>
			<i>S. krebsi</i>
			<i>O. laminatus</i>
			<i>O. irroratus</i>
			<i>O. saundersae</i>
			<i>G. ocularis</i>

TABLE 12

Main environmental factors correlated with various small mammal species in the southern Cape.

Species	Vegetation	Location	Rainfall
<i>C. asiatica</i>	fairly open grass or semi-arid scrub	flats	up to 600 mm
<i>C. duthiae</i>	probably bush or forest	flats	400+ mm
<i>A. hottentotus</i>	open grassland	flats	400+ mm
<i>E. edwardi</i>	sparse semi-arid scrub	rocky slopes	up to 600 mm
<i>M. varius</i>	dense vegetation	hillsides or flats	200+ mm
<i>C. c. cyanea</i>	grass or fynbos	rocky slopes	up to 500 mm
<i>C. c. infumata</i>	dense vegetation		500+ mm
<i>C. flavescens</i>	dense vegetation	rocky ground	400+ mm
<i>G. capensis</i>	geophytes (fynbos)	near pans on flats	400+ mm
<i>C. hottentotus</i>	sparse vegetation	flats	
<i>A. subspinosus</i>	dense scrub	rocky slopes	400+ mm
<i>A. namaquensis</i>	sparse (under 75 per cent cover) fynbos or semi-arid scrub	rocky slopes	up to 600 mm
<i>D. incommutus</i>	dense reeds or grass	near water	400+ mm
<i>P. verreauxi</i>	fynbos	rocky slopes	200+ mm
<i>R. pumilio</i>	dense vegetation	hillsides or flats	
<i>M. albicaudatus</i>	grassland	flats	400+ mm
<i>T. afra</i>	open grasslands	flats	
<i>G. paeba</i>	sparse grassland	flats or sandy slopes	up to 200 mm
<i>D. melanotis</i>	dense grassland	flats	200+ mm
<i>D. mesomelas</i>	grassland with trees or bushes	flats	200+ mm
<i>S. krebsi</i>	grassland	flats	400+ mm
<i>S. campestris</i>	open woodland with grass	flats	up to 500 mm
<i>O. laminatus</i>	grassland	rocky slopes	400+ mm
<i>O. saundersae</i>	grass or fynbos	higher rocky slopes	400+ mm
<i>O. irroratus</i>	dense (75+ per cent cover) grass, reeds or fynbos	hillsides flats	400+ mm
<i>O. unisulcatus</i>	sparse semi-arid scrub	rocky or sandy flats	up to 400 mm
		lower hillsides	
<i>G. ocularis</i>	sparse fynbos or semi-arid scrub	rocky slopes	400+ mm

the trees. On the flats, vegetation generally tends to be fairly open; the alien *Acacia* species tend to form dense thickets but with little vegetation beneath them. There are also marshy areas near the rivers (Schweitzer & Wilson 1978).

The micromammalian data (Table 7) can be divided in similar fashion. On the hillsides *Praomys verreauxi* and *Otomys saundersae* indicate scrub (here fynbos) on the upper slopes. If, as is thought likely, the subspecies of *Crocidura cyanea* represented is *C. c. cyanea*, this would indicate fynbos on the hills. *Otomys laminatus* is said to occur in grassland (Davis 1974) but possibly in this case it is the restioid element that is suggested. Equally, *O. saundersae* could represent the restioid element. *Aethomys namaquensis* indicates that the lower rocky slopes support relatively sparse scrub vegetation, which *Elephantulus edwardi* would tend to confirm. *Myosorex varius* and *Otomys irroratus* would both indicate dense vegetation, possibly proteoid in the latter species if they occurred on the hillsides. *Crocidura flavescens* indicates dense vegetation on rocky ground which is here most likely to be found on the hillsides.

The prevalence of burrowing forms on the plains is entirely consistent with the loose, sandy nature of the substrate. *Georychus capensis* suggests the possibility of one or more pans in the area, possibly the marshy areas near the rivers. The majority of species occurring on flat ground is indicative of grassland and it would seem that the coastal fynbos is largely unrepresented, except in so far as this includes a fairly high proportion of grasses. *Chrysochloris asiatica*, *Georychus capensis* and *Tatera afra* also occur in cultivated ground and their presence is consistent with the fact that much of the area either is or has been under cultivation. The relatively high proportion of *Rhabdomys pumilio* (see Table 7) suggests that this species is, in fact, very well represented in the area since it could be expected to be under-represented in *Tyto alba* pellets. Work by Jarvis & David (n.d.) indicates that *R. pumilio* has adapted to the alien *Acacia* habitat; it is also known to occur in grassland and dense streamside vegetation. In conjunction, these could help to explain its apparent abundance near Byneskranskop.

Myosorex varius, *Dasymys incomtus* and *Otomys irroratus* are all indicative of the dense grass or reeds along the banks of the river. *Dendromus mesomelas* further suggests the presence of trees in or near the damp vegetation.

It is unfortunate that the habitat preferences of some of the more numerous represented species are either unknown or catholic. *Suncus varilla* may inhabit dense vegetation, as do other soricids, but its preferences are not known. *Mus minutoides* is very adaptable but there is some indication (D. M. Avery unpublished data) that it occurs in greater numbers in owl-pellet samples from areas where agriculture is fairly extensive. It has been reported from fields and sometimes houses (Sclater 1900-1: 51), and Vesey-Fitzgerald (1966: 117) notes its occurrence in secondary and declining vegetation. It may, in fact, be that the presence of relatively large numbers of this species, and perhaps of *Suncus varilla*, indicates the occurrence of expanses of more open ground, in this case possibly fallow fields. This is suggested by the fact that individuals of

TABLE 13

Proportions of species in different habitats near Byneskranskop.

		Number	Percentage
Hillside			
<i>E. edwardi</i>	sparse vegetation	1	0,13
<i>M. varius</i> *	dense vegetation	36	4,78
<i>C. flavescens</i>	dense vegetation	25	3,32
<i>C. c. cyanea</i>	fynbos	14	1,86
<i>A. namaquensis</i>	sparse scrub	21	2,79
<i>P. verreauxi</i>	fynbos	39	5,18
<i>O. laminatus</i>	?restioid element	5	0,66
<i>O. saundersae</i>	?restioid element	5	0,66
<i>O. irroratus</i> *	dense ?proteoid element	63	8,37
		209	27,76
Plains			
<i>C. asiatica</i>	cultivated, grass	19	2,52
<i>A. hottentotus</i>	grass	1	0,13
<i>G. capensis</i>	pans, cultivated, grass	50	6,64
<i>R. pumilio</i> *	grass, <i>Acacia</i>	29	3,85
<i>M. albicaudatus</i>	grass	1	0,13
<i>T. afra</i>	cultivated, grass	62	8,23
<i>D. melanotis</i>	dense grass	22	2,92
<i>S. krebsi</i>	grass	32	4,25
		216	28,69
Riverside			
<i>M. varius</i> *	grass, fallen trees	37	4,91
<i>D. incomtus</i>	reeds, grass	1	0,13
<i>R. pumilio</i> *	grass, <i>Acacia</i>	29	3,85
<i>D. mesomelas</i>	near trees	16	2,12
<i>O. irroratus</i> *	grass, reeds	64	8,50
		147	19,52
Sundry			
<i>S. varilla</i>	76	10,09
<i>A. subspinosus</i>	6	0,80
<i>M. minutoides</i>	91	12,08
<i>R. rattus</i>	8	1,06
		181	24,04
N =		753	

* Score divided arbitrarily between two categories.

both species are small and are thus unlikely to be hunted preferentially in dense vegetation. This would be a similar situation to that found by Southern (1954) for *Strix aluco* (tawny owl) in England. *Rattus rattus* is a purely commensal species whose presence is attributable to human settlement in the area. *Acomys subspinosus* suggests dense vegetation, but whether on the edges of the scrub or on the hillsides is not known since it apparently behaves differently in coastal and inland situations.

Table 13 shows that the hillsides and the plains are approximately equally represented, with just under 30 per cent each of the total sample. The dense riverside vegetation is rather less well represented, with nearly 20 per cent of the total. The plains category would thus appear to be under-represented, but it may be that the majority of species included under the heading of 'Sundry' should be placed with the plains species, which would increase the score considerably. It may be that at Byneskranskop the majority of *Otomys irroratus* and *Myosorex varius* come from the riverside habitat, but it is not possible to assess this at the moment. The fact that the proportions of the different topographic units may not be very accurately represented in the micromammalian evidence need not be important. Except along the modern coastline topographic features have not changed during the period under discussion so that there is little merit in attempting to analyse the evidence for the physical setting. It is the vegetation that is of principal interest and this is accurately represented within the various topographic units. Examination of contemporary changes of vegetation within the different units will provide a fairly detailed overall picture of the situation in the area adjacent to the site being studied.

Cango Valley (BPB-C and NGA-B)

The Cango valley may be divided basically between the valley floor and the sides of the valley. In some places where the valley is broader, the proportion of floor to sides is clearly greater than in others. Thus, at Boomplaas, approximately one third of the area probably hunted by *Tyto alba* constitutes valley floor. At Nooitgedacht, on the other hand, no more than about a quarter of the area probably hunted is valley floor. Natural and alien vegetation occur in the vicinity of both sites. At Boomplaas extensive farming has opened up most of the alluvial valley floor, except along the Grobbelaars River and the water-furrows down each side of the valley, where larger trees and bushes occur. Directly below the cave several fields of grass with scattered walnut trees provide the equivalent of savanna vegetation. On the hillsides Dense Asteroid Shrubland, Limestone Vegetation and Mixed Bush (Moffett & Deacon 1977) succeed each other at different altitudes. Of these categories only the Limestone Vegetation has an appreciable grass element. Other vegetation types occur at higher altitudes but these are thought not to be relevant to the present study. At Nooitgedacht the succession on the hillsides also includes Dense Asteroid Shrubland and Limestone Vegetation, but with Closed Woodland in the bottom of the narrow-sided valley directly below the site. In the wider De

Hoek valley, into which the Nooitgedacht valley leads, a certain amount of agriculture has been practised on the alluvial soil. This comprises mostly the growing of fruit trees, but also involves the provision of pasture for grazing cattle. Large trees and bushes also occur along the banks of the river.

Table 14 shows that the small-mammal data reflect the greater relative importance of the hillside at Nooitgedacht compared with Boomplaas. In both

TABLE 14

Proportions of species in different habitats near Boomplaas and Nooitgedacht in the Congo valley.

		Boomplaas B-C		Nooitgedacht A-B	
		No.	%	No.	%
Valley floor					
<i>C. duthiae</i>	?bush, forest	15	1,20	8	1,00
<i>M. varius</i> *	dense vegetation	121	9,66	98	12,27
<i>C. hottentotus</i>	open vegetation	19	1,52	5	0,63
<i>D. incommutus</i>	dense waterside vegetation	—	—	2	0,25
<i>P. natalensis</i>	grass, cultivated	223	17,80	45	5,63
<i>R. pumilio</i>	dense vegetation	56	4,47	19	2,38
<i>M. albicaudatus</i>	grass	2	0,16	1	0,13
<i>D. melanotis</i>	dense grass	40	3,19	11	1,38
<i>D. mesomelas</i>	grass + trees/bushes	17	1,36	13	1,63
<i>S. krebsi</i>	grass	2	0,16	—	—
<i>S. campestris</i>	open woodland + grass	8	1,44	5	0,63
<i>O. irroratus</i> *	dense vegetation	74	5,91	78	9,76
		587	46,85	285	35,67
Hillside					
<i>E. edwardi</i>	open semi-arid scrub	6	0,48	2	0,25
<i>M. varius</i> *	dense vegetation	121	9,66	98	12,27
<i>C. c. cyanea</i>	grass, fynbos	58	4,63	18	2,25
<i>C. flavescens</i>	dense vegetation	5	0,40	4	0,50
<i>A. subspinosus</i>	dense scrub	23	1,84	43	5,38
<i>A. namaquensis</i>	open scrub	146	11,65	109	13,64
<i>P. verreauxi</i>	fynbos, ?dense	23	1,84	69	8,64
<i>O. laminatus</i>	grass	8	0,64	7	0,88
<i>O. saundersae</i>	grass, fynbos	68	5,43	33	4,13
<i>O. irroratus</i> *	dense vegetation	73	5,83	77	9,64
<i>G. ocularis</i>	open scrub	1	0,08	3	0,38
		532	42,46	463	57,95
Sundry					
<i>S. varilla</i>	23	1,84	16	2,00
<i>M. minutoides</i>	111	8,86	35	4,38
		134	10,69	51	6,38
N =	1 253		799	

* Score divided arbitrarily between two categories.

cases, however, the valley floor would appear to be heavily over-represented. This suggests either that *T. alba* has a marked preference for hunting on the valley floor or that the small-mammal biomass is actually much higher here than on the valley sides. However, as was pointed out above, disproportionate representation of the different topographic units need not inhibit accurate interpretation of the vegetation of a region. Assessment of change will, in any case, be within, rather than between, such units.

On the valley floor the species reflect the combination of both dense and more open vegetation. The former is indicated by *Myosorex varius*, *Dasymys incomtus*, *Rhabdomys pumilio*, *Dendromus melanotis* and *Otomys irroratus*. The majority of the remaining species in this category in Table 6 suggests more open vegetation. Bush or forest may be indicated by *Chlorotalpa duthiae* while more open woodland with grass, perhaps the orchards in this case, is suggested by *Dendromus mesomelas* and *Saccostomus campestris*. *Mystromys albicaudatus*, *D. melanotis* and *Steatomys krebsi* all indicate grass, possibly in wheat or fallow fields. The presence of *Praomys natalensis* is thought particularly to be an artefact of cultivation (Avery 1977). It is noticeable that this species is approximately three times as common at Boomplaas as it is at Nooitgedacht, which agrees with the greater amount of agricultural activity in the former area. It is also noticeable that most of the species which inhabit the valley floor away from the river banks are less well represented at Nooitgedacht. This is presumably an accurate reflection of the relative situation in the two areas.

On the hillsides the main indication is of scrub, which is entirely to be expected. In some cases this scrub is open (*Elephantulus edwardi*, *Aethomys namaquensis*, *Graphiurus ocellatus*) and in others denser (*Acomys subspinosus*, *Otomys irroratus*). A considerable variety of bush and scrub types is described by Moffett & Deacon (1977) and this is reflected in the variety of small mammal species occurring on the hillsides. A certain amount of grass is suggested by *Otomys laminatus* and probably also by *Crocidura c. cyanea* and *Otomys saundersae*, and grass is, in fact, a component of the Limestone Vegetation. In general, the proportions of individual species are similar at both sites. The evidence would suggest, however, that there is a higher proportion of dense vegetation at Nooitgedacht than there is at Boomplaas. This is, in fact, the case, since there is no vegetation at Nooitgedacht comparable to the more open overgrazed (Moffett & Deacon 1977: 127) scrub on the western side of the main valley opposite Boomplaas. The very much higher proportions of *Praomys verreauxi* at Nooitgedacht may suggest that this species prefers either denser vegetation or perhaps the rather wetter conditions prevailing on the eastern side of the Congo valley. The position regarding *Otomys irroratus* and *Myosorex varius* is difficult. In view of the findings of Bond *et al.* (1980), it has been considered necessary to divide the scores for the two species arbitrarily between the hillside and the valley floor. This will almost certainly prove to be an inaccurate reflection of the situation, but it is unavoidable until further data become available.

Mus minutoides and *Suncus varilla* are classed as 'Sundry' for the reasons given above for Byneskranskop 2. It is noticeable that *M. minutoides* occurs in approximately double the proportions at Boomplaas than it does at Nooitgedacht. This may be taken as further proof that this species is at an advantage in cultivated areas and more at risk on open ground.

It would appear that the micromammalian evidence provides an accurate indication of the vegetation of the Cango valley. Moreover, proportions of vegetation types within the topographic units seem to be approximately suggested by the proportions of small mammals in the samples. Greater precision and detail will only be possible when more data are available concerning the habits and ecological distribution of the small mammals.

MICROMAMMALIAN EVIDENCE FOR PALAEOENVIRONMENTAL CHANGE

The micromammalian material has been examined in three ways in an attempt to extract information concerning vegetational and climatic change. Kowalski (1971: 473) notes that in the Late Pleistocene in Europe 'the rodent-spectrum method enables better recording of even slight fluctuations in the vegetation on the basis of mammalian remains than does any other method'. This is confirmed in the present study where analysis of change in community composition has proved by far the most productive method at present. It has, therefore, received the most attention and has been considered in the greatest detail. For palaeoclimatic interpretation Kowalski (1971: 466) lists three areas of investigation. One of these concerns morphological change in certain species in response to changes in climate. Experiment has shown this to be a potentially useful line of investigation in the southern Cape as well. However, it requires a great deal more basic information regarding the reaction of modern populations than is currently available before the full potential can be realized. A second method concerns the fact that there tend to be more mammalian species represented in mild climates than in harsh ones. Investigation of changes in species diversity and community structure, which constitute extensions of the basic fact of numbers of species, suggests that information thus derived is likely to remain more general even if more data on modern communities are acquired. The third line of investigation, physical adaptations reflected in the structure of the teeth and skeleton, has been reserved for future attention.

EVIDENCE FROM COMMUNITY COMPOSITION

The various types of analysis performed and the basic procedures involved in interpretation have been described above. At this stage it is necessary only to outline the format of the present section. Each analysis is treated separately, beginning with the analyses of the individual sites and continuing with the multiple analyses. Because the species analyses may be ancillary to the levels

analyses, they have been placed first. In each case tables list variables that load highly on factors in the different analyses, together with the actual loadings. In the case of the Oblique matrices the variables are listed in the order of their loadings, with the highest first.

Boomplaas A

Species analysis

In the species analysis, species loading highly on Factor 1 (Table 15) are those that occur in higher proportions during the Holocene or minimally throughout the sequence (Fig. 8). One group of these species represents hillside vegetation. *Praomys verreauxi* and *Crocidura cyanea* (if *C. c. cyanea*) indicate scrub vegetation, probably on the higher slopes. *Aethomys namaquensis* and *Elephantulus edwardi* suggest sparse, possibly semi-arid vegetation, probably on the lower slopes. *Otomys laminatus* may indicate grass or 'grass' *sensu* Bond *et al.* (1980: 38). The valley floor is represented by another group of species, *Saccostomus campestris*, *Steatomys krebsi* and *Mystromys albicaudatus*, which

TABLE 15

Species loading highly on factors in the Varimax rotated factor matrix (A) and the Oblique rotated factor pattern matrix (B) for Boomplaas A.

Factor 1		Factor 2		Factor 3	
A:					
<i>E. edwardi</i>	0,92836	<i>C. duthiae</i>	0,89387	<i>O. unisulcatus</i>	0,86738
<i>C. flavescens</i>	0,87271	<i>M. varius</i>	0,96018		
<i>C. cyanea</i>	0,81764	<i>S. varilla</i>	0,93976		
<i>C. hottentotus</i>	0,78570	<i>D. melanotis</i>	0,97245		
<i>S. campestris</i>	0,78925	<i>O. saundersae</i>	0,89522		
<i>S. krebsi</i>	0,87093	<i>A. subspinosus</i>	0,75281		
<i>M. albicaudatus</i>	0,92848	<i>M. minutoides</i>	0,83571		
<i>O. laminatus</i>	0,75185				
<i>O. irroratus</i>	0,76388				
<i>A. namaquensis</i>	0,82348				
<i>P. verreauxi</i>	0,76681				
<i>R. pumilio</i>	0,75536				
B:					
<i>E. edwardi</i>	0,93864	<i>D. melanotis</i>	−1,00653	<i>O. unisulcatus</i>	0,74233
<i>M. albicaudatus</i>	0,92943	<i>M. varius</i>	−0,97088		
<i>S. krebsi</i>	0,90613	<i>S. varilla</i>	−0,93473		
<i>C. flavescens</i>	0,86056	<i>C. duthiae</i>	−0,87845		
<i>C. cyanea</i>	0,81309	<i>O. saundersae</i>	−0,87140		
<i>S. campestris</i>	0,80834	<i>M. minutoides</i>	−0,80355		
<i>A. namaquensis</i>	0,79290				
<i>C. hottentotus</i>	0,74969				
<i>O. laminatus</i>	0,73416				
<i>P. verreauxi</i>	0,72780				
<i>O. irroratus</i>	0,72192				
<i>R. pumilio</i>	0,71261				

88,4% of total variance accounted for. Factor correlations all low.

suggests that grass, possibly with some trees, occurred in the vicinity. *Cryptomys hottentotus* endorses the suggestion of fairly open grass on the alluvial soil along the floor of the valley. *Otomys irroratus* and *Rhabdomys pumilio* may occur in either place but both exhibit a preference for dense vegetation, particularly the former. It is perhaps likely in the present case that the majority of *Otomys irroratus* represents dense grass and reeds along the banks of the river. Equally *Rhabdomys pumilio* may occur here or elsewhere on the valley floor, depending perhaps in part on numbers of *O. irroratus*. *O. irroratus* may also have come from dense microphyllous vegetation on wetter hillslopes. Rainfall appears to have been in the region of 400–600 mm per annum.

Species loading highly on Factor 2 (Table 15) are those that occur in greater proportions during the Upper Pleistocene (Fig. 8). *Otomys saundersae* and *Acomys subspinosus* refer to the hillsides; the former indicates relatively open restioid or 'grassy' vegetation and the latter dense vegetation, probably on the higher hillsides. *Dendromus melanotis* suggests grass on the valley floor. *Chlorotalpa duthiae* is also a valley floor species that may indicate trees. *Myosorex varius* normally occurs in dense vegetation and sometimes under fallen trees and probably here represents the streamside habitat. It has, however, obviously wide tolerance and may occur in a variety of habitats at different altitudes. In general, therefore, this factor seems to indicate a more open vegetation with less scrub on the hillsides. The generally smaller size of the species may tend to confirm the more open nature of the vegetation. It would seem also that generally colder conditions must be represented.

It is relevant at this point to consider the possible relationship between *Otomys irroratus* and *Myosorex varius* since this could have a major bearing on interpretation of the data. These species apparently occur in similar habitats and, yet, shifts in their proportional representation are largely complementary. Such a seeming contradiction may indicate dependent reaction as discussed above. To some extent this could be true. *M. varius* is apparently a broad-niche species and *O. irroratus* a narrow-niche species. Thus, the latter would have the advantage within the niche to which it is adapted (see Brooks 1974), but *M. varius* would have the advantage under all other circumstances. In particular, it would be better able to adapt to environmental change. This greater adaptability may be connected with a lesser dependence on dense vegetation. It appears, for instance, that *O. irroratus* is dependent upon dense vegetation, whereas *M. varius* may be principally sensitive to atmospheric moisture levels. If this is the case, dense vegetation, frequent mists or adequate rainfall may satisfy its requirements. It has also to be borne in mind that as well as providing *O. irroratus* with protection from predators, the vegetation also constitutes the source of food. *M. varius*, on the other hand, may be nocturnal and therefore less in need of protection; it is also insectivorous and thus only indirectly dependent on the vegetation for food. Thus it seems that the relationship between the two species is complex, being partly interdependent and partly independent.

Only *Otomys unisulcatus* loads highly on Factor 3 (Table 15). It is distinguished by occurring in its highest proportions mainly during the later Upper Pleistocene. Its occurrence suggests very open vegetation, probably semi-arid scrub. In particular, it is likely to have been found on the valley floor and lower slopes of the hills.

Levels analysis

In the levels analysis the sequence is divided into three main periods, one Holocene and two Upper Pleistocene. The upper levels load highly on Factor 3 in the Varimax solution (Table 16A). These levels, which have been dated radiometrically to the Holocene, are characterized by relatively high proportions of the species that load highly on Factor 1 in the species analysis (Fig. 9). This indicates that the vegetation during the Holocene comprised scrub on the hillsides, possibly sparse and semi-arid in places and elsewhere dense and microphyllous. Fairly open grass, perhaps with some trees, on the valley floor would have been replaced by denser grass and reeds on the river-banks.

The levels loading highly on Varimax Factor 2 (Table 16A) are mainly those dated radiometrically to the late Upper Pleistocene and including the last glacial maximum. Level BOL5 alone is earlier (Fig. 9). These levels are characterized by relatively high proportions of *Otomys unisulcatus* (Fig. 9). High proportions of *Otomys saundersae* are also an important feature, as the high loading of level YOL in the Oblique solution (Table 16B; Fig. 9) indicates.

TABLE 16

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Boomplaas A.

Factor 1		Factor 2		Factor 3	
A:					
BP4	0,84357	GWA	0,75605	DGL	0,95019
OLP	0,77611	LPC	0,79799	BLD3	0,90311
OLP1	0,88619	YOL	0,83436	BL	0,94740
OLP2	0,91826	BP2	0,75382	BLA	0,86908
OLP3	0,85462	BP3	0,73674	BRL	0,81538
BOL	0,84045	BOL5	0,77767		
B:					
YOL	1,01588	BL	0,97979	OLP2	1,02529
BOL5	0,91898	DGL	0,96491	OLP1	0,94273
LPC	0,91728	BLD3	0,86622	BP4	0,87656
BP2	0,83946	BLA	0,81764	BOL	0,82354
GWA	0,83182	BRL	0,75035	OLP3	0,82152
BP3	0,82136				
LP	0,71981				

92,2% of total variance accounted for. Factor correlation moderate between Factors 1 and 2, high between Factors 1 and 3.

Crocidura cyanea is absent and *Myosorex varius* generally occurs in moderate proportions. The indication is that vegetation was generally fairly open, possibly semi-arid on the valley floor and restioid or 'grassy' on the hillsides. There must have been a certain amount of dense vegetation, especially in view of the fact that the climate was apparently fairly dry. This dense vegetation, probably grass and reeds, is most likely to have been situated along the river-banks. It is perhaps most likely to have been cold rather than aridity which drove out *C. cyanea*. If it had been the latter, it might be expected that proportions of *M. varius* and *O. irroratus* would have been lower.

The levels loading highly on Varimax Factor 1 (Table 16A) represent a period of time preceding that discussed above, that is from about 60 000 B.P. to perhaps 32 400 B.P. These levels are characterized in particular by high proportions of *Myosorex varius* and slightly lower proportions of *Otomys saundersae* (Fig. 9). This pattern is shown by level OLP2 (Fig. 9) which loads most highly in the Oblique solution. *Otomys irroratus* also occurs in fairly high proportions. The indication is that conditions were less severe than those pertaining in glacial maximum levels. An extension of dense cover is noticeable. Generally low proportions of *Cryptomys hottentotus* suggest that much of the expansion in dense vegetation occurred on the valley floor, although there may have been rather more dense scrub on the hillsides as well. The general indication is that conditions were approximately intermediate between glacial maximum and interglacial (Holocene), but that they were closer to the former than to the latter. This is suggested partly by the fact that the same two species are dominant and partly by the main division of species into a Holocene-dominant group and an Upper Pleistocene-dominant group. There is, moreover, a high correlation between the two Upper Pleistocene factors in the Oblique solution, which would seem to confirm the suggestion.

A supplementary analysis, aimed at examining the Holocene sequence in greater detail, confirmed the basic pattern already established. It further showed that conditions during the Holocene were sufficiently stable for any changes not to be detectable by present methods.

Byneskranskop 1

Species analysis

In the species analysis, species that load highly on Factor 1 (Table 17) are those that tend to occur in higher proportions in the upper half of the sequence (Fig. 10). The indication is of fairly extensive grass on the plains (*Steatomys krebsi*), dense in places (*Dendromus melanotis*), especially along the river-banks (*Myosorex varius*). The generally smaller size of the species loading on this factor may indicate relatively open vegetation as was discussed above. These species are all prominent in the Upper Pleistocene at Boomplaas A and it may be that their ascendancy at Byneskranskop 1 could indicate relatively cold and dry conditions.

TABLE 17

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Byneskranskop 1.

Factor 1		Factor 2		Factor 3	
A:					
<i>M. varius</i>	0,85083	<i>C. flavescens</i>	0,70743	<i>O. laminatus</i>	0,92387
<i>S. varilla</i>	0,88919	<i>G. capensis</i>	0,90159	<i>O. saundersae</i>	0,72222
<i>D. melanotis</i>	0,83358	<i>R. pumilio</i>	0,74821	<i>O. irroratus</i>	0,73970
<i>S. krebsi</i>	0,96512				
<i>M. minutoides</i>	0,72959				
B:					
<i>S. krebsi</i>	1,00507	<i>G. capensis</i>	0,95846	<i>O. laminatus</i>	0,87055
<i>S. varilla</i>	0,91596				
<i>M. varius</i>	0,84172				
<i>D. melanotis</i>	0,78344				

81,6% of total variance accounted for. Factor correlations low or very low.

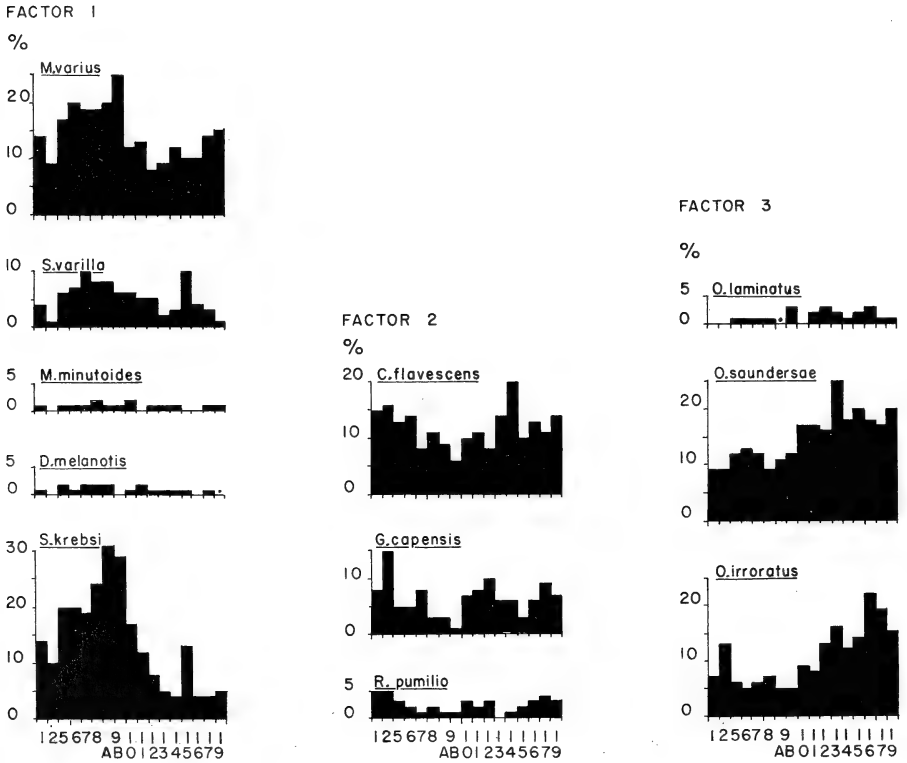


Fig. 10. Variation in percentage representation of species loading highly in the analysis of species from Byneskranskop 1 (. = less than 0,5%).

The species that load highly on Factor 2 (Table 17) show a tendency to vary inversely in proportion with the species loading highly on Factor 1 (Fig. 10). *Tatera afra* shows a similar though less distinct tendency. These species again represent the flat ground with the possibility of pans in the area (*Georychus capensis*). Low scrub, possibly coastal fynbos (*G. capensis*), together with patches of dense vegetation (*Rhodomys pumilio*) are indicated. *Tatera afra* would probably indicate more open grass. Dense vegetation, probably grass on the lower hillsides, is suggested by *Crocidura flavescens*. It is possible that conditions indicated by this factor are rather wetter than those indicated by Factor 1. The alternative is that greater seasonality is suggested by Factor 2 than by Factor 1. The Oblique solution shows *Georychus capensis* to load highly on Factor 2 and *Steatomys krebsi* most highly on Factor 1, and fynbos would require a more seasonal rainfall than would grass.

The species that load highly on Factor 3 (Table 17) tend to show a general decline in proportional representation from the bottom to the top of the sequence, but with a certain amount of recovery in level 2–4 (Fig. 10). However, whereas the first two factors referred to the plain, the third factor refers to the hillsides as well as the river-banks. The data suggest a restioid or 'grassy' vegetation on the upper and lower hillsides (*Otomys saundersae*, *Otomys laminatus*). This vegetation may perhaps have been on the sandstone hills as it is at present. *Otomys irroratus* probably indicates dense waterside vegetation but it may also suggest a dense microphyllous proteoid element which is today found on the limestone ridges. The general decline in *O. saundersae* may suggest a gradual increase in temperature on the grounds that this species was clearly at an advantage during the last glacial maximum at Boomplaas A but declined rapidly thereafter.

Levels analysis

In the levels analysis the lower levels and level 2 load highly on Factor 1 (Table 18). Radiometric dates indicate that the period represented is up to 6 500 B.P. and from approximately 3 900 to 3 400 B.P. These levels are generally characterized by high proportions of *Otomys saundersae* and, to a slightly lesser extent, *Otomys irroratus* (Fig. 11). *Tatera afra* and *Crocidura flavescens* also tend to be fairly well represented. Level 13 loads most highly in the Oblique solution (Table 18B), which suggests that a high proportion of *Otomys saundersae* is the most important element. The indication is that there was extensive dense vegetation on both the river banks and the lower hillsides and that there was grass elsewhere on the flats; a restioid or 'grassy' element and possibly a proteoid element occurred on the hills. On the basis of connotations suggested for Boomplaas A conditions would appear to have been relatively cold and wet.

Levels comprising much of the upper half of the sequence load highly on Factor 2, with level 9A loading most highly in the Oblique solution (Table 18B). This level is distinguished by high proportions of *Steatomys krebsi* and

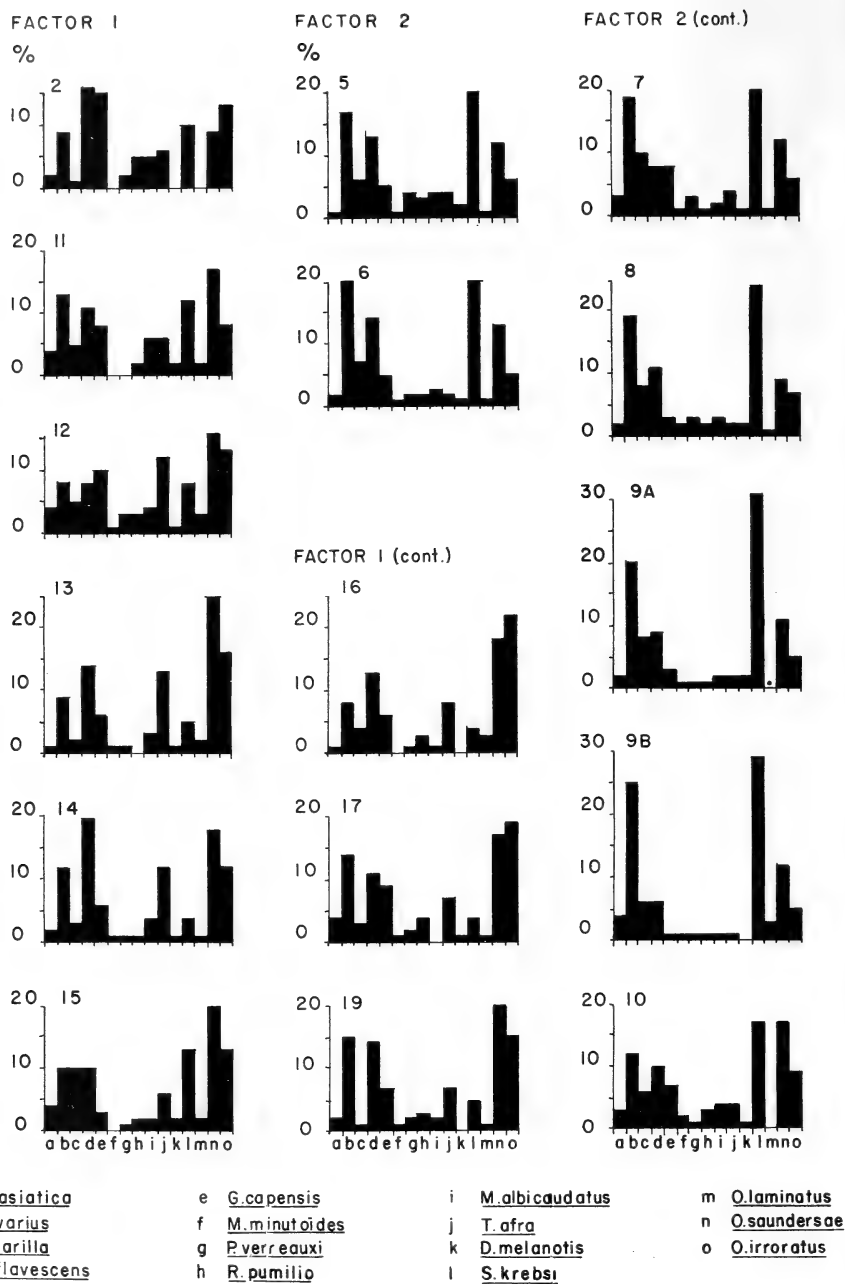


Fig. 11. Proportions of species from levels loading highly in the analysis of levels at Byneskranskop 1 (* = less than 0,5%).

TABLE 18

Levels loading highly on factors in the Varimax rotated factor matrix (A) and the Oblique rotated factor pattern matrix (B) for Byneskranskop 1.

Factor 1		Factor 2	
A:			
2	0,79895	5	0,83539
11	0,71621	6	0,84614
12	0,88697	7	0,81348
13	0,89755	8	0,92488
14	0,89078	9A	0,94780
15	0,70501	9B	0,84664
16	0,88258	10	0,71036
17	0,86701		
19	0,88958		
B:			
13	0,98908	9A	1,08319
19	0,96082	8	1,02657
16	0,96055	9B	0,85978
14	0,96000	6	0,82629
12	0,95225	5	0,81876
17	0,92879	7	0,77142
2	0,79323		

88,4% of the total variance accounted for.
Factor correlations moderate.

secondarily by fairly high proportions of *Myosorex varius*. The indication is that conditions were rather drier and probably also slightly warmer, there being fewer *O. saundersae*. There would appear to have been extensive, more or less open, grass on the flats. The reason for the replacement of *Tatera afra* by *Steatomys krebsi* as the most plentiful plains animal is not clear. It may, however, be that *S. krebsi* prefers more open grass or it could be a question of climate, with *S. krebsi* preferring drier conditions if it is similar to *S. pratensis*, which is said not to favour marshy conditions in the Namib Desert (Coetzee 1969: 32). That *S. krebsi* prefers warmer conditions is suggested by the fact that it apparently did not enter the southern Cape until after the end of the Last Glacial.

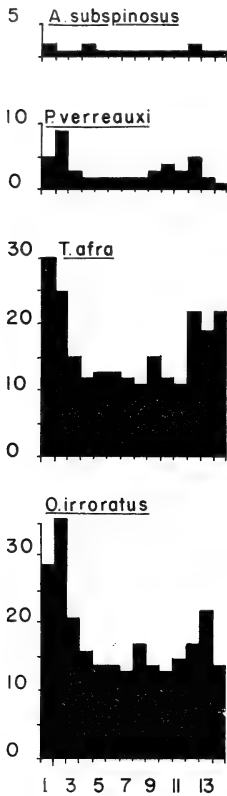
Die Kelders 1 Middle Stone Age samples

Species analysis

In the Varimax solution of the amended species analysis, species that load highly on Factor 1 (Table 19A) are those occurring in higher proportions in the upper and lower levels than in the central levels (Fig. 12). There is particular emphasis on the top two levels, except in *Acomys subspinosus* which occurs in very small numbers throughout. *Tatera afra* indicates grassy plains which may

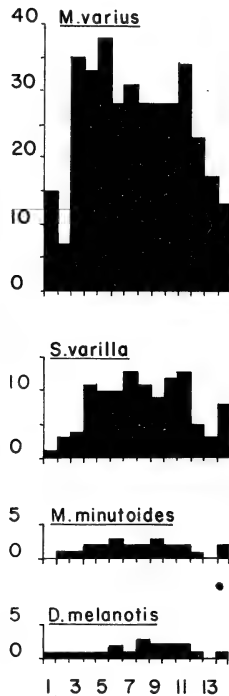
FACTOR 1

%



FACTOR 2

%



FACTOR 3

%

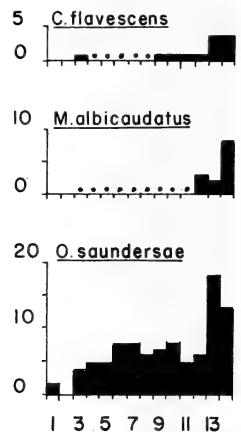


Fig. 12. Variation in percentage representation of species loading highly in the analysis of species from Die Kelders 1 M.S.A. levels (• = less than 0,5 %).

have been above or below the cave, depending upon the height of the sea at the time. *Otomys irroratus* probably indicates dense waterside vegetation, perhaps near a presently submerged marsh or lake, but it may also suggest dense scrub on hillsides. Such dense scrub is also suggested by *Acomys subspinosus*, while *Praomys verreauxi* may indicate more open scrub. The high loading of *Otomys irroratus* in the Oblique solution (Table 19B) confirms the fact that dense vegetation is a major feature of this factor. *Otomys irroratus* and *Praomys verreauxi* form part of the Holocene pattern at Boomplaas A, and it was suggested that *Tatera afra* was dominant at a relatively wet time at Byneskranskop 1. It seems likely, therefore, that relatively warm, wet conditions are indicated by this factor.

The species loading highly on Varimax Factor 2 (Table 19A) constitute the small cold element previously recognized at Boomplaas A and Byneskranskop

1. More specifically, they form the intermediate element at Boomplaas A. At Die Kelders 1 these species occur in higher proportions in the central levels, their proportions being basically the converse of those exhibited by Factor 1 species (Fig. 12). The climate was probably cooler and drier with more open vegetation containing a greater proportion of grass.

The species loading highly on Varimax Factor 3 (Table 19A) occur in higher proportions in the lowest three levels. The indications are of fairly extensive open grassland on the flats (*Myströmys albicaudatus*) with denser vegetation at the base of the hills or cliffs (*Crocidura flavescens*) and restioid or 'grassy' vegetation on the hillsides (*Otomys saundersae*). The climate was probably relatively cold.

Dendromus melanotis, which loads highly on Varimax Factor 4 (Table 19A), is distinguished by occurring in its highest proportions in level 2 (Fig. 12). This species suggests an increase in bush and perhaps even some trees. The implication would be a more moderately warm, wet climate which is not inconsistent with findings for Factor 1.

TABLE 19

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Die Kelders 1 M.S.A. levels (amended data).

Factor 1		Factor 2		Factor 3		Factor 4	
A:							
<i>T. afra</i>	0,92560	<i>M. varius</i>	0,76203	<i>C. flavescens</i>	0,96852	<i>D. mesomelas</i>	0,81893
<i>O. irroratus</i>	0,93543	<i>S. varilla</i>	0,90260	<i>M. albicaudatus</i>	0,83947		
<i>A. subspinosus</i>	0,89375	<i>D. melanotis</i>	0,85728	<i>O. saundersae</i>	0,81984		
<i>P. verreauxi</i>	0,89097	<i>M. minutoides</i>	0,92113				
B:							
<i>O. irroratus</i>	0,96112	<i>C. flavescens</i>	0,98743	<i>M. minutoides</i>	0,94282		
<i>T. afra</i>	0,93805	<i>M. albicaudatus</i>	0,78883	<i>S. varilla</i>	0,92614		
<i>P. verreauxi</i>	0,91248	<i>O. saundersae</i>	0,74763	<i>D. melanotis</i>	0,84101		
<i>A. subspinosus</i>	0,86600						

90,3 % of the total variance accounted for. Factor correlations low in all cases.

Levels analysis

In the levels analysis the central levels, 11 up to 3 or 4, load highly on Factor 1 with level 2 added in the analysis of amended data (Table 21). The distinguishing features are high proportions of *Myosorex varius* and rather lower proportions of *Suncus varilla*, *Tatera afra*, and *Otomys irroratus* (Fig. 13). The effect of amending the data is to raise the proportions of the first two species in level 2 (Fig. 13) which presumably explains why this level loads highly on Factor 1 when amended data are used. Levels 6 and 8 load most highly in the Oblique solutions (Tables 20–21) whether or not the amended data are used. It would appear that conditions were moderately cool and dry with a reduced amount of open grass on the flats but a moderate amount of restioid or 'grassy' vegetation on the hillsides.

The lowest three levels, with or without the top two levels, load highly on Factor 2. Using the original data, level 1 loads most highly on this factor in the

Oblique solution (Table 20). Here again *Myosorex varius*, *Tatera afra*, and *Otomys irroratus* are most numerous, but the latter two species have overtaken *Myosorex varius*. The fact that basically only proportions and not the species themselves have changed, may explain why the two factors are highly or moderately correlated in the Oblique solutions. It also suggests that the differences between the factors are not great. Apparently wetter conditions with much more extensive grassland are indicated by this factor. It may be that when the original data are used there is a colder and a warmer element within this factor. It is possible that *Praomys verreauxi* indicates scrub under warmer conditions in the upper levels and *Otomys saundersae* suggests restioid or 'grassy' vegetation under colder conditions in the lower levels. In this context it is notable that the two species load on different factors both at Die Kelders 1 and Boomplaas A. Moreover, *Praomys verreauxi* is barely present during glacial maximum periods at the latter site. The suggestion of milder conditions with more closed vegetation in the upper levels is endorsed by high proportions of *Otomys irroratus*. The lower levels are further distinguished by the presence of *Mystromys albicaudatus*. This is particularly noticeable when the amended data are used; the order in which the levels load in the Oblique solution (Table 21) agrees with the relative importance of *M. albicaudatus*. Proportions of

TABLE 20

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Die Kelders 1 M.S.A. levels (original data).

Factor 1		Factor 2	
A:			
3	0,73229	1	0,86177
4	0,89936	2	0,80720
5	0,86842	12	0,79641
6	0,91322	13	0,81997
7	0,91296	14	0,74322
8	0,91306		
9	0,86275		
10	0,87094		
11	0,88203		
B:			
6	1,04775	1	0,99601
8	1,04580	13	0,87854
7	1,04276	2	0,82514
4	0,99940	12	0,83845
11	0,94879	14	0,70535
10	0,90559		
5	0,89793		
9	0,88881		

92,3% of the total variance accounted for.
Factor correlation high.

TABLE 21

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Die Kelders 1 M.S.A. levels (amended data).

Factor 1		Factor 2	
A:			
2	0,78890	12	0,79377
3	0,75778	13	0,85395
4	0,89531	14	0,90062
5	0,84395		
6	0,91891		
7	0,89630		
8	0,91986		
9	0,85388		
10	0,83454		
11	0,90444		
B:			
8	1,03659	14	0,84118
6	1,02994	13	0,81722
11	0,98597	12	0,78936
7	0,97617		
4	0,96771		
9	0,88156		
5	0,85075		
10	0,83634		
2	0,76808		

89,9% of the total variance accounted for.
Factor correlation moderate.

Tatera afra are also high and there would appear to have been a great deal of grass in the area at that time. The precise differences in the habitat preferences of these two species are not known. Possibly, however, *Mystromys albicaudatus* occurred on lower ground which subsequently became submerged. It might then have been unable to compete with *Tatera afra* on the higher ground, due perhaps to unfavourable conditions such as reduced grass cover.

Coastal samples

Species analysis

In the species analysis the solutions are virtually identical and the Varimax solution, including *Steatomys krebsi*, is taken as representative (Table 22). Factor 1 is more comprehensive in the picture afforded by the greater number of species loading highly on this factor. Dense waterside vegetation is indicated by *Myosorex varius*, *Otomys irroratus*, and possibly *Rhabdomys pumilio*. Elsewhere on the flats, grass (*Dendromus melanotis*) with scattered trees or bushes (*Tatera afra*, *Dendromus mesomelas*) and possibly some open scrub (*Chryso-*

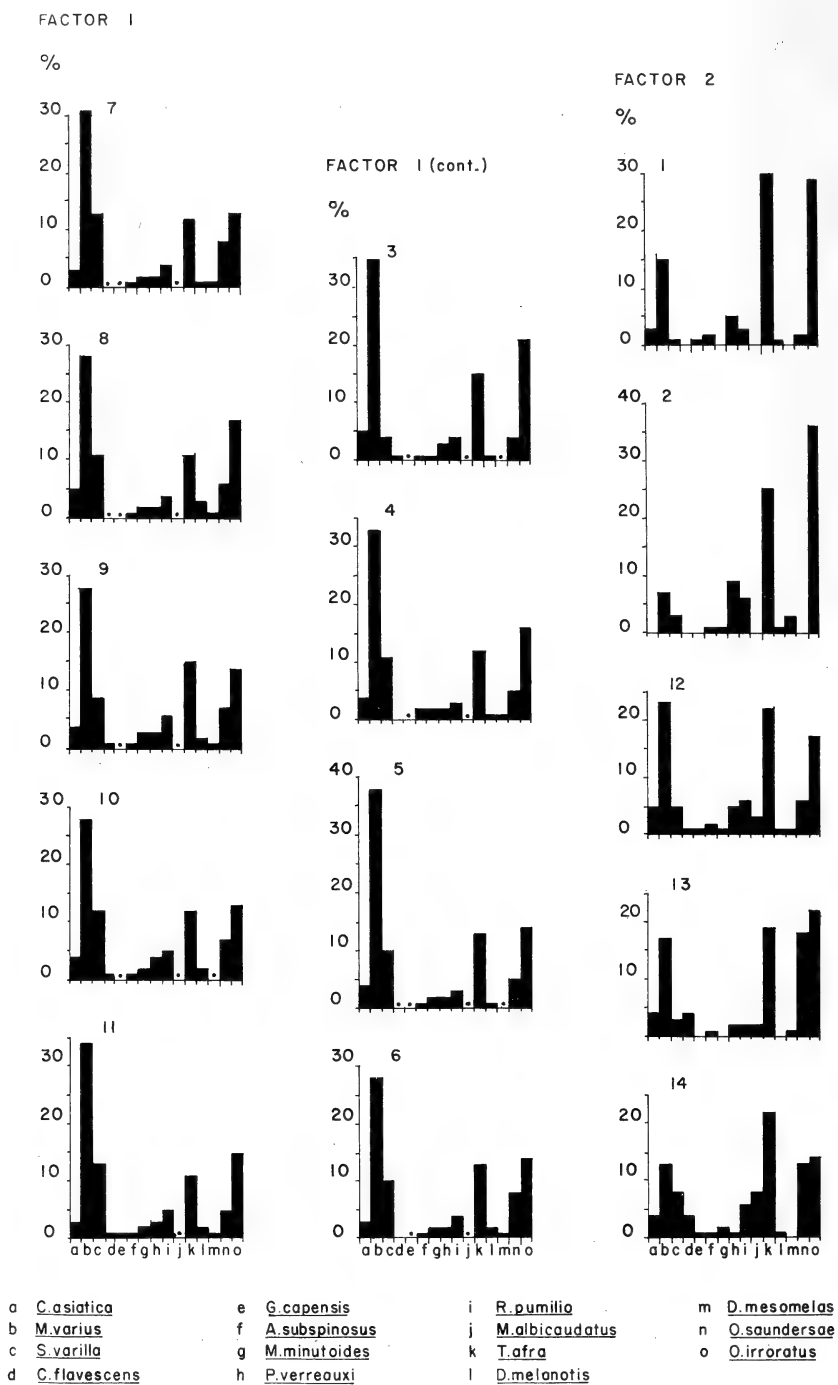


Fig. 13. Proportions of species from levels loading highly in the analysis of M.S.A. levels at Die Kelders 1 (. = less than 0,5%).

TABLE 22

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for coastal samples (*Steatomys krebsi* included).

Factor 1		Factor 2	
A:			
<i>C. asiatica</i>	0,96655	<i>C. flavescentis</i>	0,96267
<i>M. varius</i>	0,96153	<i>G. capensis</i>	0,86370
<i>S. varilla</i>	0,93595	<i>S. krebsi</i>	0,84076
<i>D. melanotis</i>	0,94581	<i>M. albicaudatus</i>	0,73592
<i>D. mesomelas</i>	0,90984	<i>O. laminatus</i>	0,76755
<i>T. afra</i>	0,88450		
<i>O. irroratus</i>	0,94844		
<i>A. subspinosus</i>	0,93390		
<i>M. minutoides</i>	0,95332		
<i>P. verreauxi</i>	0,90731		
<i>R. pumilio</i>	0,93716		
B:			
<i>C. asiatica</i>	0,96698	<i>C. flavescentis</i>	0,99900
<i>M. varius</i>	0,96251	<i>G. capensis</i>	0,82996
<i>M. minutoides</i>	0,95298	<i>S. krebsi</i>	0,82315
<i>O. irroratus</i>	0,94370		
<i>D. melanotis</i>	0,94333		
<i>S. varilla</i>	0,93407		
<i>A. subspinosus</i>	0,93054		
<i>R. pumilio</i>	0,93053		
<i>D. mesomelas</i>	0,89963		
<i>P. verreauxi</i>	0,89579		
<i>T. afra</i>	0,86892		

83,4% of the total variance accounted for. Factor correlation very low.

chloris asiatica) is indicated. On the hillsides *Acomys subspinosus* and *Praomys verreauxi* suggest scrub. The climate would appear to have been at least moderately warm with a rainfall in excess of 400 mm per annum. The picture indicated by Factor 2 is dense vegetation (*Crocidura flavescens*), and probably grass (*Otomys laminatus*) on the lower hillslopes. Grass (*Mystromys albicaudatus*, *Steatomys krebsi*) is also indicated on the flats, together with pans and perhaps some scrub (*Georchus capensis*).

In the Oblique solution, *Chrysochloris asiatica* and *Myosorex varius* load most highly on Factor 1 whether or not *Steatomys krebsi* is included (Tables 22–23). *Crocidura flavescens* is central to the pattern represented by Factor 2. The indication is that central aspects of Factor 1 are sparser vegetation and a drier climate. For Factor 2 denser vegetation and rather wetter conditions are indicated.

In general, the species loading highly on Factor 1 are those which occur either in higher proportions in the DK1 M.S.A. levels or in approximately

TABLE 23

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for coastal samples (*Steatomys krebsi* excluded).

Factor 1		Factor 2	
A:			
<i>C. asiatica</i>	0,96553	<i>C. flavescens</i>	0,96345
<i>M. varius</i>	0,95874	<i>G. capensis</i>	0,86511
<i>S. varilla</i>	0,93186	<i>M. albicaudatus</i>	0,76555
<i>D. melanotis</i>	0,94620	<i>O. laminatus</i>	0,76059
<i>D. mesomelas</i>	0,91990		
<i>T. afra</i>	0,88604		
<i>O. irroratus</i>	0,94861		
<i>A. subspinosus</i>	0,94549		
<i>M. minutoides</i>	0,95184		
<i>P. verreauxi</i>	0,91106		
<i>R. pumilio</i>	0,93963		
B:			
<i>C. asiatica</i>	0,96461	<i>C. flavescens</i>	0,98828
<i>M. varius</i>	0,95723	<i>G. capensis</i>	0,83015
<i>M. minutoides</i>	0,94863		
<i>A. subspinosus</i>	0,94815		
<i>O. irroratus</i>	0,94521		
<i>D. melanotis</i>	0,94185		
<i>R. pumilio</i>	0,93417		
<i>S. varilla</i>	0,92605		
<i>D. mesomelas</i>	0,91540		
<i>P. verreauxi</i>	0,90101		
<i>T. afra</i>	0,87401		

83,7% of the total variance accounted for. Factor correlation very low.

equal proportions throughout. The species that load highly on Factor 2 are those which occur in higher proportions at BNK1.

Levels analysis

In the levels analysis, most of the BNK1 levels load highly on Factor 1, whether or not *Steatomys krebsi* is included (Tables 24–25). Because BNK1 is dated radiometrically to the postglacial period, it may be assumed that this factor represents relatively warm conditions. In the Oblique solution, level 6 loads most highly when *S. krebsi* is included, whereas level 11 loads most highly when it is omitted. Since level 11 is the second highest loading level in the first analysis, it may be considered the most generally representative. This is probably explainable in terms of the fact that in the BNK1 analysis, level 11 tends to be intermediate. Level 6 is distinguished by equally high proportions of *Myosorex varius* and *Steatomys krebsi* and slightly lower proportions of *Crociodura flavescens* and *Otomys saundersae*. Level 11, without *Steatomys krebsi*, is distinguished by high proportions of *Otomys saundersae* and slightly lower

proportions of *Myosorex varius* and *Crocidura flavescens*. The omission of *Steatomys krebsi* would appear, therefore, only to promote a slight change in emphasis. The indication is of relatively cold, dry conditions with reduced dense streamside vegetation, but fairly extensive dense vegetation on the lower hillsides. Extensive grass on the plains and upper hillsides is indicated.

The majority of the DK1 M.S.A. levels loads highly on Factor 2 with levels 7 and 8 loading most highly in the Oblique solution whether or not *Steatomys krebsi* is included (Tables 24–25). Since the DK1 M.S.A. levels are thought to be Upper Pleistocene in age, this factor should represent rather colder condi-

TABLE 24

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for coastal samples (*Steatomys krebsi* included).

Factor 1		Factor 2		Factor 3	Factor 4
A:					
BNK1:	1	0,92329	DK1 M.S.A:	3	0,93394
	2	0,86238		4	0,98497
	5	0,90716		5	0,98596
	6	0,93519		6	0,97390
	7	0,89096		7	0,98565
	8	0,86791		8	0,98093
	9A	0,87869		9	0,97217
	9B	0,78084		10	0,97645
	10	0,95231		11	0,96473
	11	0,97358		12	0,83609
	12	0,90922		13	0,71645
	13	0,86676			
	14	0,91204			
	15	0,90712			
	16	0,82248			
	17	0,79429			
	19	0,86448			
B:					
BNK1:	6	0,98901	DK1 M.S.A:	7	1,02513
	11	0,98452		8	1,01752
	10	0,96754		4	1,01722
	9A	0,96334		5	1,00761
	8	0,94502		6	0,99812
	5	0,94372		10	0,98780
	7	0,92715		9	0,97808
	1	0,92101		11	0,96408
	15	0,88448		3	0,87517
	14	0,85260		12	0,73803
	12	0,84869			
	9B	0,83782			
	2	0,81650			
	13	0,79294			
	19	0,78708			
	16	0,74114			

91,6% of the total variance accounted for. Factor correlations low in all cases.

TABLE 25

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for coastal samples (*Steatomys krebsi* excluded).

Factor 1			Factor 2		Factor 3		Factor 4	
A:								
BNK1:	1	0,91154	DK1 M.S.A:	3	0,88514			
	2	0,87867		4	0,97039			
	5	0,86818		5	0,96722			
	6	0,90341		6	0,95426			
	7	0,83742		7	0,97045			
	8	0,80173		8	0,97866			
	9A	0,81366		9	0,96167			
	10	0,92246		10	0,95671			
	11	0,96692		11	0,95212			
	12	0,92068		12	0,78523			
	13	0,91092						
	14	0,95965						
	15	0,87502						
	16	0,85971						
	17	0,82840						
	19	0,89241						
B:								
BNK1:	11	1,00342	DK1 M.S.A:	8	1,03686			
	14	0,99307		7	1,01440			
	2	0,96243		4	1,01118			
	1	0,95995		5	0,99676			
	12	0,94240		9	0,98918			
	13	0,94231		6	0,98714			
	6	0,93010		10	0,97629			
	10	0,92427		11	0,97431			
	19	0,92199		3	0,85559			
	5	0,87770		12	0,72414			
	16	0,85570						
	15	0,84938						
	17	0,81348						
	7	0,81472						
	9A	0,78855						
	8	0,78172						

91,5% of the total variance accounted for. Moderate correlation between Factors 1 and 2, otherwise low.

tions than those represented by Factor 1. Levels 7 and 8 are distinguished by high proportions of *Myosorex varius* and rather lower proportions of *Suncus varilla*, *Tatera afra*, and *Otomys irroratus*. The high proportion of *Myosorex varius* in levels loading on Factors 1 and 2 explains the moderate correlation between these two factors. The fact that *Otomys irroratus* also occurs in a fairly high proportion possibly suggests that Factor 2 represents a situation where dense waterside vegetation makes up a relatively large part of the overall vegetation. *Tatera afra* indicates grass elsewhere on the flats but the significance of *Suncus varilla* is unfortunately not known. It seems that basically the

difference between the two factors is one of degree as far as the vegetation is concerned. The only clear difference in kind appears to lie in the proportions of *Crocidura flavescens* which is virtually absent from the DK1 M.S.A. levels. There is, therefore, no connotation of dense vegetation on the lower hillsides for Factor 2.

Holocene and modern samples

Species analysis

In the species analysis the grouping of the species is similar to that encountered in other analyses (Table 26). Factor 1 indicates a moderate amount of dense waterside vegetation (*Myosorex varius*) with grass elsewhere on the flats (*Dendromus* spp.) and lower hillsides (*Otomys laminatus*). Also on the hillsides, scrub is suggested by *Praomys verreauxi*. A moderate climate is indicated. Factor 2 suggests a colder climate with grass or open scrub on the upper hillsides (*Otomys saundersae*), dense vegetation on the lower hillsides (*Crocidura flavescens*), and open grassland on the flat ground (*Mystromys albicaudatus*). Factor 3 indicates more or less open grassland with some bushes (*Steatomys krebsi*), although it is not clear how this factor differs from the others climatically.

In the Oblique solution, the species central to the pattern represented by Factor 1 are *Mus minutoides*, *Dendromus melanotis* and, to a lesser extent, *Myosorex varius* (Table 26B). These species are those that are interpreted as

TABLE 26

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Holocene and modern samples.

Factor 1		Factor 2		Factor 3	
A:					
<i>M. varius</i>	0,90679	<i>C. flavescens</i>	0,89048	<i>S. krebsi</i>	0,93227
<i>S. varilla</i>	0,82715	<i>M. albicaudatus</i>	0,90012		
<i>D. melanotis</i>	0,92403	<i>O. saundersae</i>	0,77251		
<i>D. mesomelas</i>	0,79299				
<i>O. laminatus</i>	0,72755				
<i>M. minutoides</i>	0,92981				
<i>P. verreauxi</i>	0,74619				
<i>R. pumilio</i>	0,85238				
B:					
<i>M. minutoides</i>	0,94258	<i>M. albicaudatus</i>	0,88385	<i>S. krebsi</i>	0,92996
<i>D. melanotis</i>	0,93562	<i>C. flavescens</i>	0,86102		
<i>M. varius</i>	0,90510				
<i>S. varilla</i>	0,83443				
<i>D. mesomelas</i>	0,81630				
<i>R. pumilio</i>	0,81603				

82,6% of the total variance accounted for. Factor correlations very low.

representing interstadial conditions in the Boomplaas A analysis. *Mystromys albicaudatus* and *Crocidura flavescens* load highly on Factor 2. The distinction between these two factors is basically the same as that occurring in the previous analysis of coastal samples. Factor 1 appears to represent cooler drier conditions with sparser vegetation than does Factor 2. Factor 3 is distinguished by a high loading of *Steatomys krebsi*. The reason for this is almost certainly topographic and, as such, of little use in the present work.

Levels analysis

In the levels analysis the BPA levels load highly on Factor 1, together with BNK1 level 19 in the Varimax solution (Table 27A). In the Oblique solution BPA level BRL4UA loads most highly (Table 27B). The BPA levels are

TABLE 27

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Holocene and modern samples.

Factor 1		Factor 2		Factor 3		Factor 4	
A:							
BPA: BLD3A	0,80190	BNK1: 1	0,79037	BNK2	0,84484		
BL	0,86097	5	0,91847	BPB-C	0,90962		
BLA	0,84449	6	0,90805	NGA-B	0,88355		
BRL	0,84450	7	0,92357	GLEN	0,86964		
BRL4UA	0,91946	8	0,92301				
BRL4	0,92291	9A	0,95951				
BRL5	0,90189	9B	0,95343				
BRL6	0,92471	10	0,86978				
BRL7	0,92105	11	0,82139				
CL1	0,88865	12	0,73449				
BNK 1-19	0,71169	15	0,81116				
B:							
BPA: BRL4UA	0,97970			BPB-C	0,89277	BNK1: 9B	-1,11151
BL	0,97658			NGA-B	0,86808	9A	-1,00763
BRL4	0,95835			BNK2	0,86490	7	-0,96127
BRL	0,92726			GLEN	0,82436	6	-0,86357
BRL7	0,90905					5	-0,84630
BRL6	0,86040					11	-0,83457
BLD3A	0,85334					15	-0,83247
BLA	0,84857					10	-0,78009
BRL5	0,80609						
CL1	0,71308						

92,1% of the total variance accounted for. Moderate correlations between Factors 1 and 4, otherwise very low.

characterized by an extremely high proportion of *Otomys irroratus*, but in level BRL4UA this is particularly noticeable. Although this is probably due to the small size of the sample, the same pattern is discernible in level BL, which loads next most highly. Generally *Crocidura flavescens* is of secondary importance and the implication of this factor is extensive dense vegetation both on the river-banks and along the lower hillsides.

The majority of the BNK1 levels loads highly on Factor 2 (Varimax). (Table 27A). Level 9B loads most highly, followed by level 9A, in the Oblique solution (Table 27B). The sample from level 9B is again very small but the picture provided by level 9A is very similar. The distinguishing features in this case are high proportions of *Steatomys krebsi* together with rather lesser proportions of *Myosorex varius*. *Otomys saundersae* is the only other species of

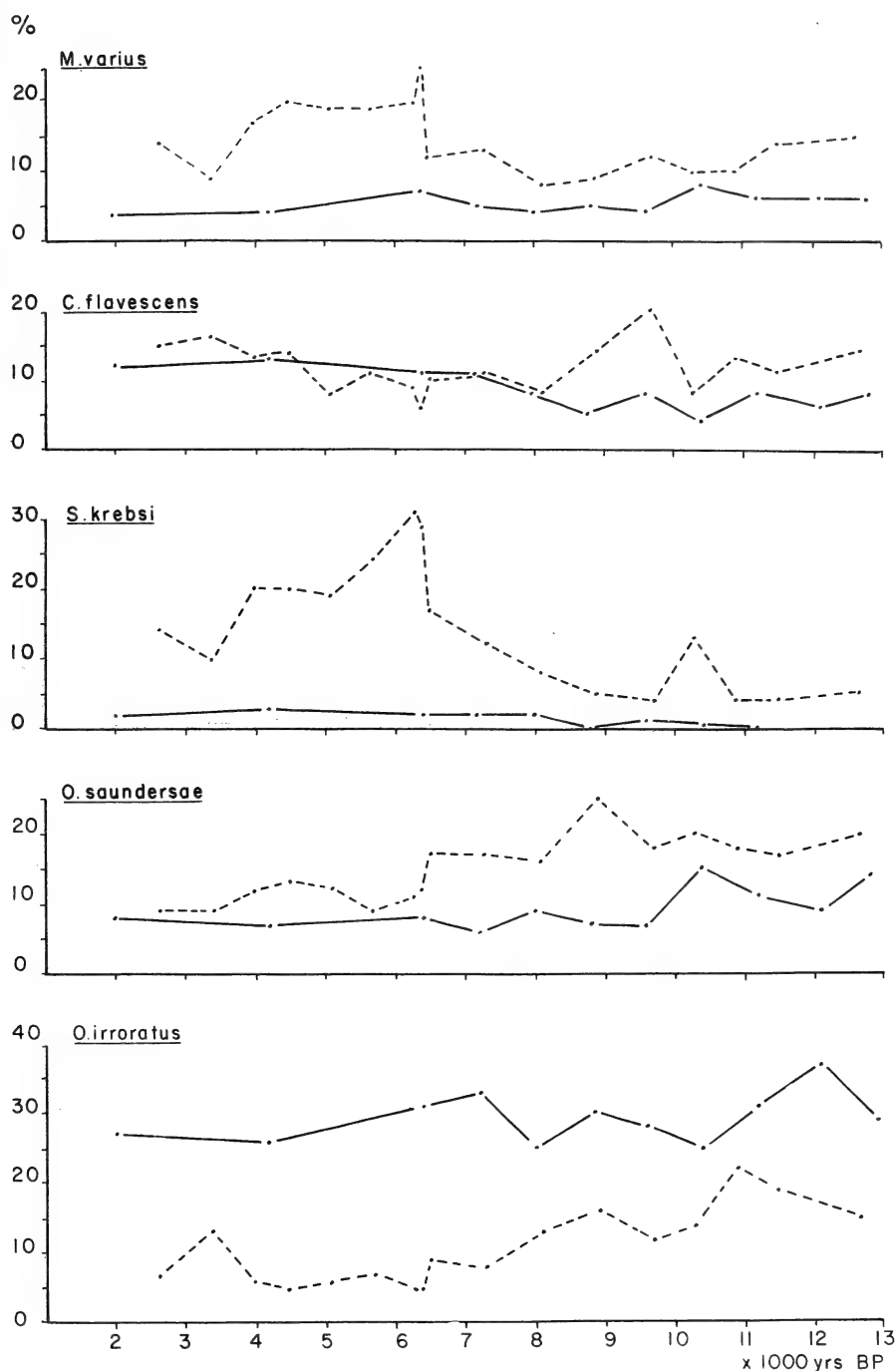


Fig. 14. Correlation of Boomplaas A levels BLD3A to CL1 with the Byneskranskop 1 sequence. (Solid line = Boomplaas A; dashed line = Byneskranskop 1.)

any importance. The moderate correlation between these two factors is probably due to the fact that *O. saundersae* occurs in approximately equal proportions at both sites (Fig. 14). It would appear that this factor indicates drier conditions than does the previous factor. The basic distinction is probably geographic or topographic in origin. That is to say, large proportions of *Steatomys krebsi* are made possible by the presence of open plains, whereas the high proportions of *Otomys irroratus* are probably due to the relatively small amount of flat ground on the valley floor. However, the fact that *Myosorex varius* is present in higher proportions than is *Otomys irroratus* in one area and not in the other does indicate a difference between the two. Factor 2, then, represents a relatively reduced streamside habitat with more or less open grass elsewhere on the flat. It probably also represents drier conditions than Factor 1.

The modern samples all load highly on Factor 3, with BPB-C loading most highly in the Oblique solution (Table 27). The distinguishing features here are a high proportion of *Myosorex varius* and a fairly high proportion of *Otomys irroratus*. *Mus minutoides* also occurs in much higher proportions than it does in the Holocene samples. This is thought to be an artefact of the practice of agriculture but, in any case, this species is too unspecific in its habitat requirements to be of use for interpretation. The indication is that there is a great concentration on the streamside habitat in this factor. Since there are no levels loading highly on the fourth factor, it was not possible to determine the environmental connotations of this factor.

Upper Pleistocene and modern samples

Species analysis

In the analysis of species the division of species is very similar to that observed in the coastal analysis described above (Table 28). *Myosorex varius*, *Otomys irroratus* and, possibly, *Rhabdomys pumilio* attest dense waterside vegetation. *Acomys subspinosus* and *Praomys verreauxi* indicate scrub on the hillsides, while *Dendromys* spp. suggest grass on the lower ground, with some trees or bushes in the case of *D. mesomelas*. Factor 2 indicates restioid or 'grassy' vegetation on the upper hillsides (*Otomys saundersae*), dense vegetation on the lower hillsides (*Crocidura flavescens*) and open grassland on the flats (*Mystromys albicaudatus*). On the basis of the interpretation of the Boomplaas A analysis, it would seem likely that Factor 1 represents rather warmer interstadial conditions while Factor 2 represents full glacial conditions.

In the Oblique solution *Dendromys mesomelas*, followed by *Rhabdomys pumilio*, *Mus minutoides*, and *Praomys verreauxi*, is central to the pattern represented by Factor 1 (Tables 3-4). Only *Otomys saundersae* loads highly on Factor 2. Since *Rhabdomys pumilio* and *Praomys verreauxi* both appear to be part of the Holocene element at Boomplaas A, this would tend to confirm the suggestion that Factor 1 represents milder conditions than does Factor 2. It may also be that wetter conditions are indicated.

TABLE 28

Species loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Upper Pleistocene and modern samples.

Factor 1		Factor 2	
A:			
<i>M. varius</i>	0,71515	<i>C. flavescens</i>	0,71424
<i>S. varilla</i>	0,86903	<i>M. albicaudatus</i>	0,77563
<i>D. melanotis</i>	0,81438	<i>O. saundersae</i>	0,89907
<i>D. mesomelas</i>	0,90757		
<i>O. irroratus</i>	0,84780		
<i>A. subspinosus</i>	0,84536		
<i>M. minutoides</i>	0,93138		
<i>P. verreauxi</i>	0,91645		
<i>R. pumilio</i>	0,92568		
B:			
<i>D. mesomelas</i>	0,97707	<i>O. saundersae</i>	0,95466
<i>R. pumilio</i>	0,94764		
<i>M. minutoides</i>	0,93837		
<i>P. verreauxi</i>	0,93625		
<i>S. varilla</i>	0,83498		
<i>O. irroratus</i>	0,81435		
<i>A. subspinosus</i>	0,79736		
<i>D. melanotis</i>	0,75197		

81,9% of the total variance accounted for. Factor correlation low.

In general, the species that load most highly on Factor 1 occur in approximately equal proportions at both sites or are rather better represented at DK1. The species that load highly on Factor 2 are those that occur in greater proportions at BPA.

Levels analysis

In the levels analysis the two solutions are slightly different (Table 29). The reason for this is not known, except that it may have been caused by the moderate correlation between Factor 1 and Factors 3 and 4. Because of this correlation it was considered that the Oblique solution was more likely to be correct and it was therefore utilized for interpretation. Apart from BPB and C, the levels here loading highly on Factor 1 are those that, in the analyses of individual sites, loaded highly on factors considered to represent interstadial conditions. Level OLP3 loads most highly on this factor with a very high proportion of *Myosorex varius* and with *Otomys saundersae* of secondary importance. As has been suggested above, this probably represents a moderately dry, cold climate.

NBC level YSL loads highly on Factor 2 and this level is dated radiometrically to the last maximum of the Last Glacial (Table 29). This factor may thus be considered to represent glacial conditions. The very high proportions of

Otomys saundersae tend to support this suggestion. The only other species to occur in any numbers is *Mystromys albicaudatus*, so that the general impression is of extensive grassland on the flats and restioid or 'grassy' vegetation on the hillsides.

DK1 M.S.A. level 2, which loads highly on Factor 3, is distinguished by very high proportions of *Otomys irroratus*, with *Praomys verreauxi* and *Myosorex varius* the only other species to occur in even moderate proportions. Extensive dense waterside vegetation and scrub on the hillsides are indicated. By comparison with the Boomplaas A analysis, it would appear that this factor most nearly represents Holocene or interglacial conditions. It is probable, therefore, that conditions were relatively warm as well as relatively wet.

TABLE 29

Levels loading highly on factors in the Varimax rotated factor matrix (A) and Oblique rotated factor pattern matrix (B) for Upper Pleistocene and modern samples.

Factor 1		Factor 2		Factor 3		Factor 4	
A:							
BPA: YOL	0,86001	BPA: OLP3	0,71777	DK1 M.S.A: 2	0,77182		
BP2	0,82808	DK1 M.S.A: 3	0,80435				
BP3	0,89820	4	0,95147				
BP4	0,82391	5	0,91220				
OLP	0,76818	6	0,94493				
OLP1	0,73770	7	0,94014				
BOL	0,76889	8	0,95415				
BOL1	0,96818	9	0,91429				
BOL4	0,93851	10	0,88617				
BOL5	0,88003	11	0,94384				
OCH	0,91062	BNK2	0,77737				
LOH	0,90113	BPB-C	0,89406				
KRM1A: 15	0,71570	NGA-B	0,82756				
DK1 M.S.A: 13	0,85308						
NBC: YSL	0,87318						
YGL	0,88311						
B:							
BPA: OLP3	0,98289	NBC: YSL	0,71206	DK1 M.S.A: 2	0,91355	KRM 1A: 15	0,88213
BP1	0,97444					32	0,87497
OLP2	0,96506					BPA: BOL4	0,86883
OLP1	0,88768					BOL1	0,80520
DK1 M.S.A: 4	0,87412					BP3	0,71704
5	0,85567						
7	0,84874						
8	0,84319						
6	0,83297						
11	0,81468						
9	0,80619						
10	0,79499						
BPA: OLP	0,79118						
BOL	0,74424						
BPB-C	0,74415						
BPA: BP4	0,73993						

92,8% of the total variance accounted for. Moderate correlation between Factor 1 and Factors 3 and 4, otherwise low.

KRM1A level 15 loads most highly on Factor 4 (Table 29). High proportions of *Otomys irroratus* and moderately high proportions of *Otomys saundersae* distinguish this level. The only other species to occur in some quantity in these levels are *Crocidura flavescens* and *Myosorex varius*. It would seem that wet and fairly cold conditions are indicated, with extensive dense vegetation at the waterside and a certain amount on the lower hillsides. The BPA levels that load highly on this factor are some that load highly on the glacial maximum

factor in the Boomplaas A analysis. It is possible that the difference between this factor and Factor 2 is largely topographic. It is probable, however, that rather warmer, wetter conditions are represented by Factor 4 compared with those represented by Factor 2. Certainly *Crocidura flavescens* would not normally be expected in high proportions in very cold conditions. It is also probable that the apparent anomalies in the KRM1A data are due to the incompleteness of the available samples. The moderate correlation between Factor 1 and Factors 3 and 4 is probably due to the fact that variations are in proportion rather than in species.

EVIDENCE FROM MEAN SIZE VARIATION

That populations of certain species tend to vary in mean size of individual members is an observed fact. It is particularly suggested that these changes represent responses to differing temperatures. Bergmann's Rule, as has been noted above, states that within a particular species those individuals living in warmer climates will tend to have a smaller body mass than those individuals living in colder climates. The converse of this should be that if there is variation in mean body mass of populations living in the same place but at different times in the past, this must indicate warmer or cooler climates at the relevant times. In other words, if body mass can be correlated with temperature it should be possible to use this method to provide direct evidence of past temperature fluctuations. In fact, Kowalski (1971) quotes a study by Sych (1965) in which increase in the body size of a fossil hare from Poland is shown to indicate a gradual decrease in mean temperature of about 10 °C during the Pliocene and early Pleistocene.

In order to achieve such results it is clear that basic data must be available for modern representatives of the species concerned. Initially it must be established whether or not the species does, in fact, behave according to Bergmann's Rule, since not all species do. If the species exhibits a consistent negative or positive response, it is necessary then to ascertain the scale of changes involved. Such an adequate data base is not currently available for the species being examined in the present study, so that a quantitative assessment cannot yet be made. The subfossil records show, however, that real changes have taken place which can be correlated in a broad way with known climatic change. In particular, the shrews *Crocidura flavescens* and *Myosorex varius* provide good evidence. Limited data for *Tatera afra* suggests that this species may also be useful but the trend in *Aethomys namaquensis* does not appear to be correlated with known climatic fluctuations.

The nature of the evidence forthcoming from *Cryptomys hottentotus* is more problematic. The mean size of individual in this species varies quite considerably in samples of different ages. It would appear, therefore, that once it has been established what causes the changes, *C. hottentotus* should be of considerable use in palaeoenvironmental interpretation. Climatic change may normally be reflected in temperature change, but Tchernov (1968) has shown

TABLE 30

Size variation in mandibles of *Crocidura flavescens* from Boomplaas A and B.

		A: height of ascending ramus					B: depth of body mandible				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	
BPA:	DGL	70	6,9–8,7	7,74	0,36	0,09	106	2,4–3,5	2,86	0,23	
	BLD3	70	7,2–8,5	7,80	0,31	0,07	131	2,5–3,5	2,90	0,21	
	BL	51	7,2–9,1	7,88	0,38	0,11	69	2,5–3,4	2,95	0,21	
	BLA	36	7,4–9,0	8,12	0,37	0,13	54	2,5–3,4	3,02	0,19	
	BRL	72	7,4–9,2	8,25	0,38	0,09	96	2,6–3,8	3,10	0,23	
	CL	50	7,7–9,0	8,34	0,39	0,10	56	2,7–3,7	3,16	0,23	
	GWA	4	8,2–9,2	8,43			22	3,0–3,5	3,25	0,17	
	LP	16	7,9–8,9	8,41	0,35	0,19	69	2,9–3,7	3,24	0,22	
	YOL	4	7,6–9,0	8,60			8	2,9–3,6	3,25	0,29	
	BP4	8	8,0–9,0	8,48	0,44	0,37	29	2,7–3,5	3,05	0,17	
	OLP	6	8,0–9,2	8,52	0,45	0,47	12	2,7–3,3	3,01	0,19	
	OLP1	6	7,9–9,2	8,63	0,46	0,48	5	3,0–3,4	3,22	0,18	
	OLP2	26	7,7–9,5	8,44	0,44	0,18	40	2,7–3,6	3,19	0,19	
OLP3	13	8,2–8,8	8,47	0,23	0,14	42	2,8–3,6	3,11	0,23		
	BOL	11	7,2–9,0	8,17	0,50	0,33	31	2,6–3,5	3,03	0,21	
	OCH	12	7,9–8,9	8,38	0,30	0,19	19	2,9–3,6	3,13	0,18	
	BPB	6	7,3–8,3	7,70	0,40	0,41	7	2,5–3,2	2,80	0,23	

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 31

Size variation in mandibles of *Crocidura flavescens* from Boomplaas A upper levels.

		A: height of ascending ramus					B: depth of body mandible				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	
Unit DGL											
DGL1	15	7,6–8,5	8,01	0,26	0,15	14	2,7–3,4	2,92	0,20	
DGL2	31	6,9–8,7	7,66	0,39	0,14	44	2,6–3,5	2,88	0,20	
BLD	9	7,2–8,3	7,66	0,33	0,25	16	2,0–3,2	2,73	0,30	
BLD2	8	7,3–8,5	7,75	0,40	0,33	12	2,4–3,3	2,94	0,25	
BLD2A	7	7,3–7,8	7,63	0,16	0,15	20	2,6–3,1	2,81	0,15	
Unit BLD3											
BLD3	39	7,3–8,5	7,77	0,31	0,10	75	2,4–3,4	2,85	0,20	
BLD3A	31	7,2–8,5	7,84	0,32	0,12	56	2,5–3,5	2,96	0,23	
Unit BRL											
BRL	18	7,5–8,8	8,23	0,38	0,19	22	2,6–3,3	3,07	0,19	
BRL2	17	7,6–8,9	8,18	0,34	0,18	25	2,7–3,7	3,04	0,20	
BRL4/4A	6	7,7–8,4	8,15	0,27	0,29	14	2,7–3,3	3,01	0,19	
BRL5	11	7,7–8,7	8,12	0,38	0,25	11	2,8–3,4	3,03	0,18	
BRL6	20	7,4–9,2	8,41	0,42	0,19	24	2,6–3,8	3,22	0,28	
Unit CL											
BRL7	19	7,9–9,0	8,46	0,39	0,19	20	2,8–3,6	3,25	0,21	
CL1	13	7,9–8,7	8,18	0,30	0,18	16	2,7–3,6	3,16	0,20	
CL2	9	8,1–8,9	8,50	0,31	0,24	8	2,8–3,7	3,20	0,31	
CL3BG	9	7,7–8,8	8,13	0,43	0,33	12	2,8–3,1	2,98	0,11	

Measurements in mm.

95% = 95% confidence interval for the mean.

Age	D: length of lower tooth row				E: length of mandible plus incisor								
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%			
6,3	5,91	0,18	0,07	6	11,4–12,6	12,08	0,40	0,42	9	16,8–19,2	18,32	0,85	0,28
5,5	6,04	0,19	0,06	8	11,5–13,1	12,26	0,53	0,45	6	17,4–19,3	17,97	0,72	0,75
5,3	6,04	0,17	0,06	13	11,8–13,1	12,27	0,38	0,23	25	16,5–20,0	18,40	0,77	0,32
6,7	6,20	0,26	0,10	6	11,9–12,4	12,00	0,31	0,33	9	17,1–19,1	18,12	0,66	0,51
5,8	6,27	0,22	0,05	19	12,0–13,6	12,71	0,43	0,21	20	17,9–20,5	19,19	0,73	0,34
6,8	6,43	0,21	0,08	11	13,0–13,9	13,30	0,27	0,18	11	19,0–20,9	20,06	0,72	0,48
6,9	6,54	0,21	0,18										
7,0	6,55	0,25	0,13	1	(13,2)				3	19,0–20,4	19,70		
6,7	6,53			2	12,2–13,6	12,90			3	18,3–20,6	19,40		
6,6	6,35	0,25	0,26						1	(18,8)			
6,5	6,47			1	(13,1)				2	19,9–20,4	20,15		
6,7	6,45								1	(18,7)			
7,0	6,56	0,19	0,09	6	13,1–14,2	13,47	0,50	0,52	6	19,5–21,3	20,45	0,67	0,70
7,0	6,48	0,28	0,14	8	12,6–13,9	13,35	0,47	0,40	8	19,0–21,2	20,29	0,88	0,74
6,5	6,24	0,25	0,21	2	12,7–13,2	12,95			3	18,4–19,6	19,10		
6,8	6,27	0,23	0,18	3	12,3–13,0	12,67			3	19,2–19,7	19,53		
6,2	5,88	0,19	0,24	3	11,5–12,0	11,73			4	17,4–18,3	17,83		

h of M ₁₋₃				D: length of lower tooth row					E: length of mandible plus incisor				
age	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
-6,1	5,95			1	(12,3)				4	17,3-19,0	18,33		
-6,3	5,93	0,18	0,10	3	11,4-12,1	11,87			3	16,8-19,2	17,93		
-6,2	5,85												
-6,0	5,93			2	12,0-12,6	12,30			2	18,6-19,2	18,90		
-6,0	5,88	0,11	0,14										
-6,4	6,03	0,19	0,07	6	11,5-13,1	12,22	0,57	0,60	3	17,5-18,0	17,67		
-6,5	6,05	0,21	0,11	2	12,0-12,8	12,40			3	17,4-19,3	18,27		
-6,4	6,19	0,17	0,10	3	12,4-12,9	12,70			4	18,6-19,5	19,08		
-6,8	6,21	0,22	0,11	6	12,2-13,5	12,68	0,44	0,18	6	18,2-19,7	18,90	0,53	0,56
-6,7	6,28	0,26	0,16	5	12,0-13,0	12,42	0,45	0,49	3	17,9-20,2	18,77		
-6,5	6,31	0,18	0,16	2	12,7-13,0	12,85			2	19,2-19,5	19,35		
-6,6	6,37	0,22	0,12	3	12,9-13,6	13,17			5	18,8-20,5	19,82	0,68	0,84
-6,8	6,42	0,21	0,16	2	13,2-13,3	13,25			5	19,0-20,9	19,94	0,83	1,03
-6,7	6,39	0,23	0,17	5	13,0-13,6	13,24	0,26	0,32	2	19,0-20,7	19,85		
-6,7	6,50	0,25	0,30	3	13,1-13,9	13,40			3	19,8-20,9	20,30		
-6,7	6,45	0,14	0,15	1	(13,4)				1	(20,3)			

TABLE 30

Size variation in mandibles of *Crociodura flavescens* from Boomplaas A and B.

		A: height of ascending ramus					B: depth of body mandible					C: length of lower tooth row					D: length of lower tooth row					E: length of mandible plus incisor				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
BPA:	DGL	70	6,9-8,7	7,74	0,36	0,09	106	2,4-3,5	2,86	0,23	0,09	6	11,4-12,6	12,08	0,40	0,42	9	16,8-19,2	18,32	0,85	0,28					
	BLD3	70	7,2-8,5	7,80	0,31	0,07	131	2,5-3,5	2,90	0,21	0,06	8	11,5-13,1	12,26	0,53	0,45	6	17,4-19,3	17,97	0,72	0,75					
	BL	51	7,2-9,1	7,88	0,38	0,11	69	2,5-3,4	2,95	0,21	0,06	13	11,8-13,1	12,27	0,38	0,23	25	16,5-20,0	18,40	0,77	0,32					
	BLA	36	7,4-9,0	8,12	0,37	0,13	54	2,5-3,4	3,02	0,19	0,06	6	11,9-12,4	12,00	0,31	0,33	9	17,1-19,1	18,12	0,66	0,51					
	BRL	72	7,4-9,2	8,25	0,38	0,09	96	2,6-3,8	3,10	0,23	0,05	19	12,0-13,6	12,71	0,43	0,21	20	17,9-20,5	19,19	0,73	0,34					
	CL	50	7,7-9,0	8,34	0,39	0,10	56	2,7-3,7	3,16	0,23	0,08	11	13,0-13,9	13,30	0,27	0,18	11	19,0-20,9	20,06	0,72	0,48					
	GWA	4	8,0-9,2	8,43			22	3,0-3,5	3,25	0,17	0,08															
	LP	16	7,9-8,9	8,41	0,35	0,19	69	2,9-3,7	3,24	0,22	0,13	1	(13,2)				3	19,0-20,4	19,70							
	YOL	4	7,6-9,0	8,60			8	2,9-3,6	3,25	0,29	0,13	2	12,2-13,6	12,90			3	18,3-20,6	19,40							
	BP4	8	8,0-9,0	8,48	0,44	0,37	29	2,7-3,5	3,05	0,17	0,06						1	(18,8)								
	OLP	6	8,0-9,2	8,52	0,45	0,47	12	2,7-3,3	3,01	0,19	0,09	1	(13,1)				2	19,9-20,4	20,15							
	OLP1	6	7,9-9,2	8,63	0,46	0,48	5	3,0-3,4	3,22	0,18	0,06						1	(18,7)								
	OLP2	26	7,7-9,5	8,44	0,44	0,18	40	2,7-3,6	3,19	0,19	0,09	6	13,1-14,2	13,47	0,50	0,52	6	19,5-21,3	20,45	0,67	0,70					
	OLP3	13	8,2-8,8	8,47	0,23	0,14	42	2,8-3,6	3,11	0,23	0,14	8	12,6-13,9	13,35	0,47	0,40	8	19,0-21,2	20,29	0,88	0,74					
	BOL	11	7,2-9,0	8,17	0,50	0,33	31	2,6-3,5	3,03	0,21	0,08	2	12,7-13,2	12,95			3	18,4-19,6	19,10							
	OCH	12	7,9-8,9	8,38	0,30	0,19	19	2,9-3,6	3,13	0,18	0,08	3	12,3-13,0	12,67			3	19,2-19,7	19,53							
BPB		6	7,3-8,3	7,70	0,40	0,41	7	2,5-3,2	2,80	0,23	0,14	3	11,5-12,0	11,73			4	17,4-18,3	17,83							

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 31

Size variation in mandibles of *Crociodura flavescens* from Boomplaas A upper levels.

		A: height of ascending ramus					B: depth of body mandible					C: length of lower tooth row					D: length of lower tooth row					E: length of mandible plus incisor				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
Unit DGL																										
DGL1		15	7,6-8,5	8,01	0,26	0,15	14	2,7-3,4	2,92	0,20	0,09	1	(12,3)				4	17,3-19,0	18,33							
DGL2		31	6,9-8,7	7,66	0,39	0,14	44	2,6-3,5	2,88	0,20	0,10	3	11,4-12,1	11,87			3	16,8-19,2	17,93							
BLD		9	7,2-8,3	7,66	0,33	0,25	16	2,0-3,2	2,73	0,30	0,10															
BLD2		8	7,3-8,5	7,75	0,40	0,33	12	2,4-3,3	2,94	0,25	0,10	2	12,0-12,6	12,30			2	18,6-19,2	18,90							
BLD2A		7	7,3-7,8	7,63	0,16	0,15	20	2,6-3,1	2,81	0,15	0,09															
Unit BLD3																										
BLD3		39	7,3-8,5	7,77	0,31	0,10	75	2,4-3,4	2,85	0,20	0,09	6	11,5-13,1	12,22	0,57	0,60	3	17,5-18,0	17,67							
BLD3A		31	7,2-8,5	7,84	0,32	0,12	56	2,5-3,5	2,96	0,23	0,11	2	12,0-12,8	12,40			3	17,4-19,3	18,27							
Unit BRL																										
BRL		18	7,5-8,8	8,23	0,38	0,19	22	2,6-3,3	3,07	0,19	0,10	3	12,4-12,9	12,70			4	18,6-19,5	19,08							
BRL2		17	7,6-8,9	8,18	0,34	0,18	25	2,7-3,7	3,04	0,20	0,11	6	12,2-13,5	12,68	0,44	0,18	6	18,2-19,7	18,90	0,53	0,56					
BRL4/4A		6	7,7-8,4	8,15	0,27	0,29	14	2,7-3,3	3,01	0,19	0,16	5	12,0-13,0	12,42	0,45	0,49	3	17,9-20,2	18,77							
BRL5		11	7,7-8,7	8,12	0,38	0,25	11	2,8-3,4	3,03	0,18	0,16	2	12,7-13,0	12,85			2	19,2-19,5	19,35							
BRL6		20	7,4-9,2	8,41	0,42	0,19	24	2,6-3,8	3,22	0,28	0,12	3	12,9-13,6	13,17			5	18,8-20,5	19,82	0,68	0,84					
Unit CL																										
BRL7		19	7,9-9,0	8,46	0,39	0,19	20	2,8-3,6	3,25	0,21	0,11	2	13,2-13,3	13,25			5	19,0-20,9	19,94	0,83	1,03					
CL1		13	7,9-8,7	8,18	0,30	0,18	16	2,7-3,6	3,16	0,20	0,17	5	13,0-13,6	13,24	0,26	0,32	2	19,0-20,7	19,85							
CL2		9	8,1-8,9	8,50	0,31	0,24	8	2,8-3,7	3,20	0,31	0,15	3	13,1-13,9	13,40			3	19,8-20,9	20,30							
CL3BG		9	7,7-8,8	8,13	0,43	0,33	12	2,8-3,1	2,98	0,11	0,09	1	(13,4)				1	(20,3)								

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 32

Size variation in mandibles of *Crocidura flavescens* from coastal sites

		A: height of ascending ramus					B: depth of body of mandible				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	
BNK1: 5	.	27	6,9–8,2	7,54	0,36	0,14	31	2,5–3,2	2,83	0,20	
19	.	16	7,2–8,3	7,75	0,41	0,22	32	2,5–3,2	2,81	0,19	
DK1: L.S.A.12	.	3	7,7–8,0	7,87			8	2,7–3,1	2,86	0,14	
M.S.A.4	.	6	6,9–7,6	7,33	0,24	0,25	11	2,5–2,8	2,74	0,10	
6	.	10	7,3–8,4	7,73	0,30	0,21	15	2,6–3,1	2,78	0,12	
10	.	5	7,3–8,1	7,67	0,35	0,43	8	2,6–3,2	2,81	0,18	
KRM1A: 6	.	2	(8,5)				7	3,1–3,5	3,39	0,15	
15	.	6	8,0–8,9	8,37	0,39	0,41	17	2,9–3,6	3,21	0,21	
22	.	4	7,2–8,4	7,80			14	2,7–3,4	3,04	0,19	
32	.	3	7,3–8,1	7,70			8	2,7–3,4	3,04	0,23	
NBC: YSL	.	13	8,1–8,7	8,41	0,19	0,11	47	2,5–3,7	3,21	0,22	
YGL	.	17	7,4–9,1	8,21	0,46	0,23	37	2,8–3,5	3,15	0,20	
BNK2	.	25	6,6–7,8	7,29	0,32	0,13	38	2,1–3,2	2,61	0,26	

Measurements in mm.

95 = 95% confidence interval for the mean.

that in the case of *Spalax ehrenbergi* (Palestine mole-rat) in Israel the correlation is with rainfall. Demonstrable changes in *Cryptomys hottentotus* in the present study may perhaps also be attributable to rainfall fluctuation. Data on such a possible correlation have not yet been accumulated (J. U. M. Jarvis 1979 pers. comm.) but De Graaff (1981) notes a tendency for this species to be geographically variable in size.

Crocidura flavescens

Five parameters were measured in *Crocidura flavescens* as was described above. Tables 30–32 give the resultant data for different populations and Figures 16–21 present the same data in graphic form. Figure 15 illustrates the variation in the means of the various parameters throughout the sequence at Boomplaas A. It is clear that there is considerable variation in the mean sizes of the various populations and, in particular, the good sequence at Boomplaas A shows clear trends.

Figure 15 shows that the pattern of size change in the mandible of *C. flavescens* at Boomplaas A is very similar in all the parameters measured. This would suggest that, in fact, the mandible was changing in overall size rather than in one aspect alone. Until such time as the nature of the relationship of the size of the mandible to overall body mass is established for this species, it will be assumed that a larger mandible indicates greater body mass. In general terms, on this basis, *C. flavescens* is shown to be larger during the Upper Pleistocene than during the Holocene. The only exception is level BOL where the means are smaller than those for the earliest part of the Holocene sequence. Larger samples for level BOL may clarify this situation and it will be important to discover whether the lower BOL levels follow the same trend or

Length of M_{1-3}					D: length of lower tooth row					E: length of mandible plus incisor				
Age	\bar{X}	s	95%		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
-6,1	5,78	0,19	0,08		23	10,9-12,2	11,70	0,39	0,17	31	16,4-18,7	17,70	0,63	0,23
-6,2	5,87	0,19	0,08		10	11,3-12,7	11,89	0,47	0,34	15	16,5-19,2	18,11	0,79	0,44
-6,0	5,86	0,16	0,15		5	10,6-12,1	11,62	0,61	0,76	3	18,0-18,4	18,27		
-5,7	5,55									3	16,8-17,4	17,07		
-6,0	5,85				1	(11,5)				3	17,3-17,6	17,47		
					1	(12,0)				2	17,9-18,3	18,10		
-6,6	6,40													
-6,4	6,30	0,17	0,13		4	12,1-12,8	12,43			6	17,9-20,6	19,28	0,88	0,93
-6,4	6,23													
-6,4	6,14	0,17	0,21		3	12,3-12,5	12,40			3	18,4-18,9	18,67		
-6,8	6,44	0,18	0,10		4	12,7-13,8	13,40	0,48	0,77	5	18,6-21,0	20,26	0,95	1,18
-6,7	6,40	0,29	0,15		3	13,3-14,0	13,60			7	18,7-20,8	19,89	0,66	0,61
-6,1	5,65	0,25	0,10		19	10,4-12,2	11,50	0,50	0,24	24	15,9-18,3	17,16	0,62	0,26

whether specimens from these levels will be larger. In the length of M_{1-3} and depth of mandible means are highest during the period from about 25 000 B.P. to about 14 000 B.P., that is the last glacial maximum (Figs 16-17). In the height of the ascending ramus the mean is higher at the beginning of this period. In all three parameters an earlier high occurs in levels OLP1 or OLP2 when means are highest for length of lower tooth row (Fig. 18) and length of mandible plus incisor (Fig. 19). The data for level OLP2 are reliable, being based on a good sample, but those from level OLP1 require improvement. In view of the correlation between large size and glacial maximum, it seems safe to assume tentatively that the species is behaving in accordance with Bergmann's Rule. This being the case, it would appear that there is an indication during the Upper Pleistocene of two main cold periods separated by a milder period, and that the Holocene was considerably warmer than almost all of the preceding period represented at Boomplaas A.

From about 14 000 B.P. onwards there is a continuous trend towards smaller means in the various parameters up to and including the modern sample from Boomplaas B. That this trend is far from smooth is shown by the means for the upper levels at Boomplaas A (Figs. 20-21). There are perhaps two main periods of fluctuation. The first is in the lowest postglacial levels, CL3BG to BRL5, and the second is in the uppermost levels, BLD2A to DGL1, and Boomplaas B. In the first it is the height of the ascending ramus that fluctuates most noticeably. This parameter displays moderate coefficients of variation (Table 33), which suggests that real fluctuation rather than changes in population composition are being monitored. Such fluctuations are perhaps to be expected during a period of climatic change. During the later period of fluctuation, on the other hand, the greatest amplitude is found in the depth of

TABLE 32

Size variation in mandibles of *Crociodura flavescens* from coastal sites

	N	A: height of ascending ramus				N	B: depth of body of mandible			
		Range	\bar{X}	s	95%		Range	\bar{X}	s	95%
BNK1: 5	27	6,9-8,2	7,54	0,36	0,14	31	2,5-3,2	2,83	0,20	
19	16	7,2-8,3	7,75	0,41	0,22	32	2,5-3,2	2,81	0,19	
DK1: L.S.A.12	3	7,7-8,0	7,87			8	2,7-3,1	2,86	0,14	
M.S.A.4	6	6,9-7,6	7,33	0,24	0,25	11	2,5-2,8	2,74	0,10	
6	10	7,3-8,4	7,73	0,30	0,21	15	2,6-3,1	2,78	0,12	
10	5	7,3-8,1	7,67	0,35	0,43	8	2,6-3,2	2,81	0,18	
KRM1A: 6	2	(8,5)				7	3,1-3,5	3,39	0,15	
15	6	8,0-8,9	8,37	0,39	0,41	17	2,9-3,6	3,21	0,21	
22	4	7,2-8,4	7,80			14	2,7-3,4	3,04	0,19	
32	3	7,3-8,1	7,70			8	2,7-3,4	3,04	0,23	
NBC: YSL	13	8,1-8,7	8,41	0,19	0,11	47	2,5-3,7	3,21	0,22	
YGL	17	7,4-9,1	8,21	0,46	0,23	37	2,8-3,5	3,15	0,20	
BNK2	25	6,6-7,8	7,29	0,32	0,13	38	2,1-3,2	2,61	0,26	

Measurements in mm.

95 = 95% confidence interval for the mean.

that in the case of *Spalax ehrenbergi* (Palestine mole-rat) in Israel the correlation is with rainfall. Demonstrable changes in *Cryptomys hottentotus* in the present study may perhaps also be attributable to rainfall fluctuation. Data on such a possible correlation have not yet been accumulated (J. U. M. Jarvis 1979 pers. comm.) but De Graaff (1981) notes a tendency for this species to be geographically variable in size.

Crociodura flavescens

Five parameters were measured in *Crociodura flavescens* as was described above. Tables 30-32 give the resultant data for different populations and Figures 16-21 present the same data in graphic form. Figure 15 illustrates the variation in the means of the various parameters throughout the sequence at Boomplaas A. It is clear that there is considerable variation in the mean sizes of the various populations and, in particular, the good sequence at Boomplaas A shows clear trends.

Figure 15 shows that the pattern of size change in the mandible of *C. flavescens* at Boomplaas A is very similar in all the parameters measured. This would suggest that, in fact, the mandible was changing in overall size rather than in one aspect alone. Until such time as the nature of the relationship of the size of the mandible to overall body mass is established for this species, it will be assumed that a larger mandible indicates greater body mass. In general terms, on this basis, *C. flavescens* is shown to be larger during the Upper Pleistocene than during the Holocene. The only exception is level BOL where the means are smaller than those for the earliest part of the Holocene sequence. Larger samples for level BOL may clarify this situation and it will be important to discover whether the lower BOL levels follow the same trend or

	N	D: length of lower tooth row				N	E: length of mandible plus incisor			
		Range	\bar{X}	s	95%		Range	\bar{X}	s	95%
BNK1: 5	23	10,9-12,2	11,70	0,39	0,17	31	16,4-18,7	17,70	0,63	0,23
19	10	11,3-12,7	11,89	0,47	0,34	15	16,5-19,2	18,11	0,79	0,44
DK1: L.S.A.12	5	10,6-12,1	11,62	0,61	0,76	3	18,0-18,4	18,27		
M.S.A.4	1	(11,5)				3	16,8-17,4	17,07		
6	1	(12,0)				3	17,3-17,6	17,47		
10						2	17,9-18,3	18,10		
KRM1A: 6	4	12,1-12,8	12,43			6	17,9-20,6	19,28	0,88	0,93
15	3	12,3-12,5	12,40			3	18,4-18,9	18,67		
22	4	12,7-13,8	13,40	0,48	0,77	5	18,6-21,0	20,26	0,95	1,18
32	3	13,3-14,0	13,60			7	18,7-20,8	19,89	0,66	0,61
NBC: YSL	19	10,4-12,2	11,50	0,50	0,24	24	15,9-18,3	17,16	0,62	0,26
YGL										
BNK2										

whether specimens from these levels will be larger. In the length of M_1 and depth of mandible means are highest during the period from about 25 000 B.P. to about 14 000 B.P., that is the last glacial maximum (Figs 16-17). In the height of the ascending ramus the mean is higher at the beginning of this period. In all three parameters an earlier high occurs in levels OLP1 or OLP2 when means are highest for length of lower tooth row (Fig. 18) and length of mandible plus incisor (Fig. 19). The data for level OLP2 are reliable, being based on a good sample, but those from level OLP1 require improvement. In view of the correlation between large size and glacial maximum, it seems safe to assume tentatively that the species is behaving in accordance with Bergmann's Rule. This being the case, it would appear that there is an indication during the Upper Pleistocene of two main cold periods separated by a milder period, and that the Holocene was considerably warmer than almost all of the preceding period represented at Boomplaas A.

From about 14 000 B.P. onwards there is a continuous trend towards smaller means in the various parameters up to and including the modern sample from Boomplaas B. That this trend is far from smooth is shown by the means for the upper levels at Boomplaas A (Figs. 20-21). There are perhaps two main periods of fluctuation. The first is in the lowest postglacial levels, CL3BG to BRL5, and the second is in the uppermost levels, BLD2A to DGL1, and Boomplaas B. In the first it is the height of the ascending ramus that fluctuates most noticeably. This parameter displays moderate coefficients of variation (Table 33), which suggests that real fluctuation rather than changes in population composition are being monitored. Such fluctuations are perhaps to be expected during a period of climatic change. During the later period of fluctuation, on the other hand, the greatest amplitude is found in the depth of

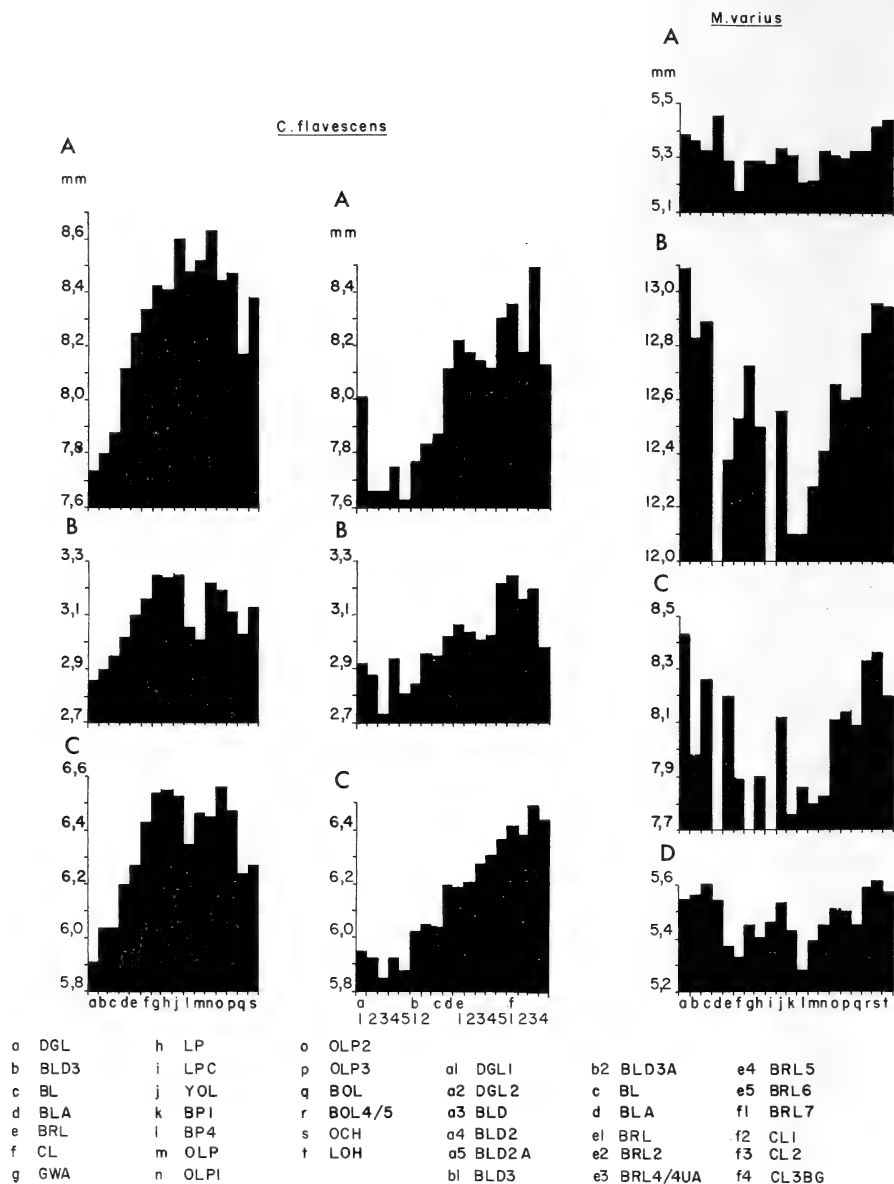


Fig. 15. Variation in the means of parameters measured in *Crocidura flavescens* and *Myosorex varius* from Boomplaas A. See Tables 30 and 36 for details.

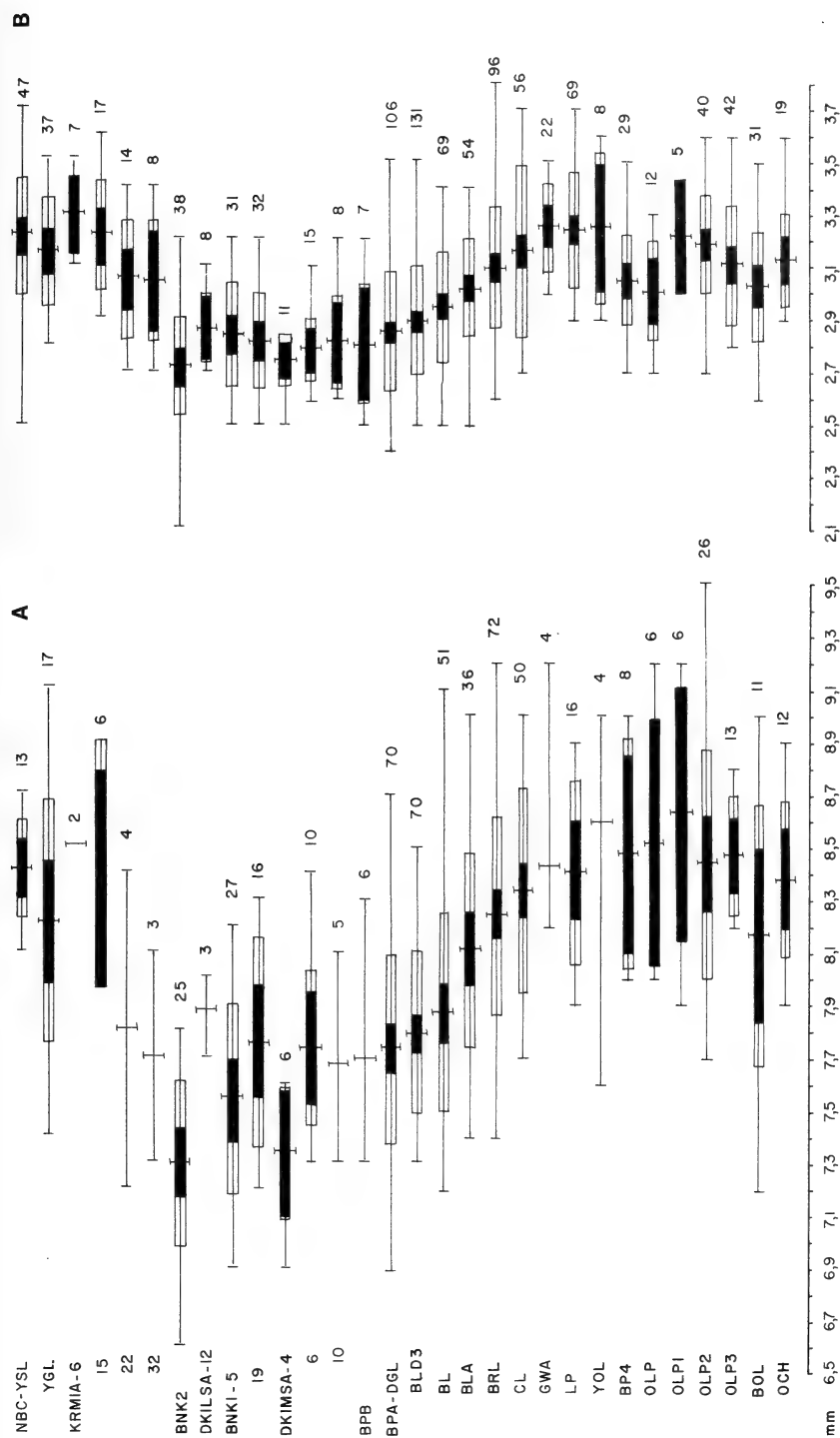


Fig. 16. Variation in parameter A, height of ascending ramus, and parameter B, depth of mandible, in *Crocidura flavescens* from various sites.

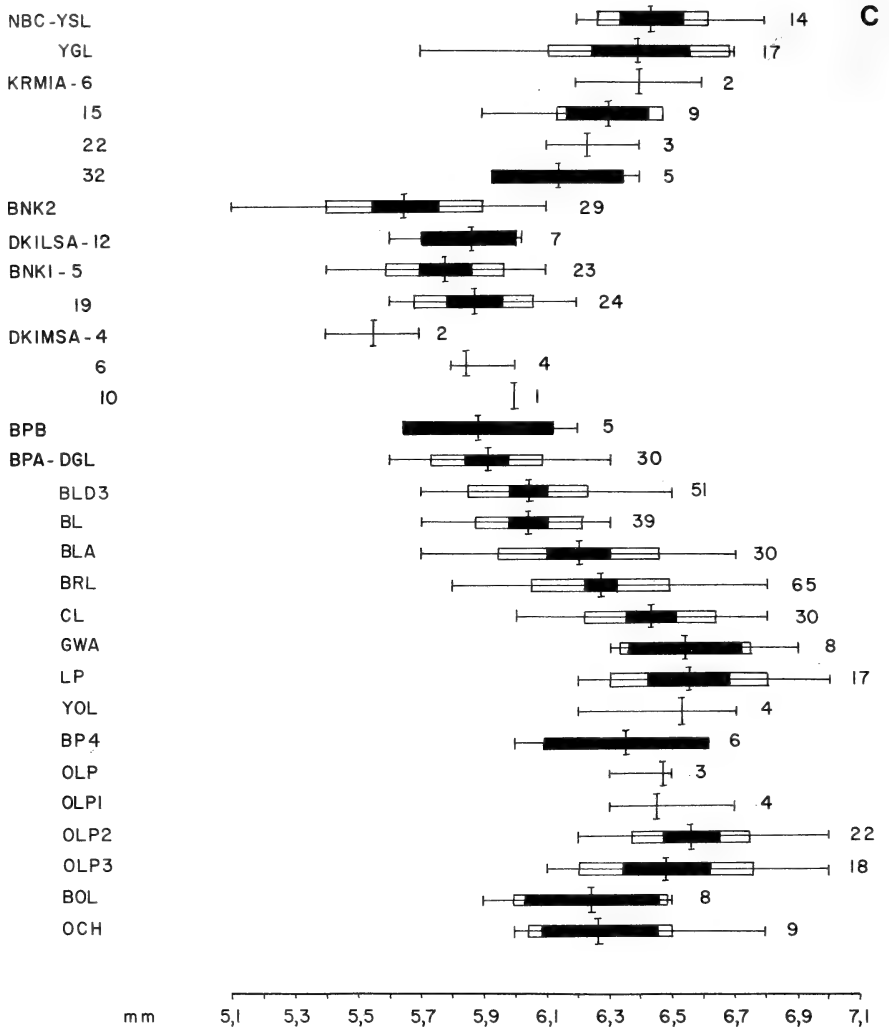
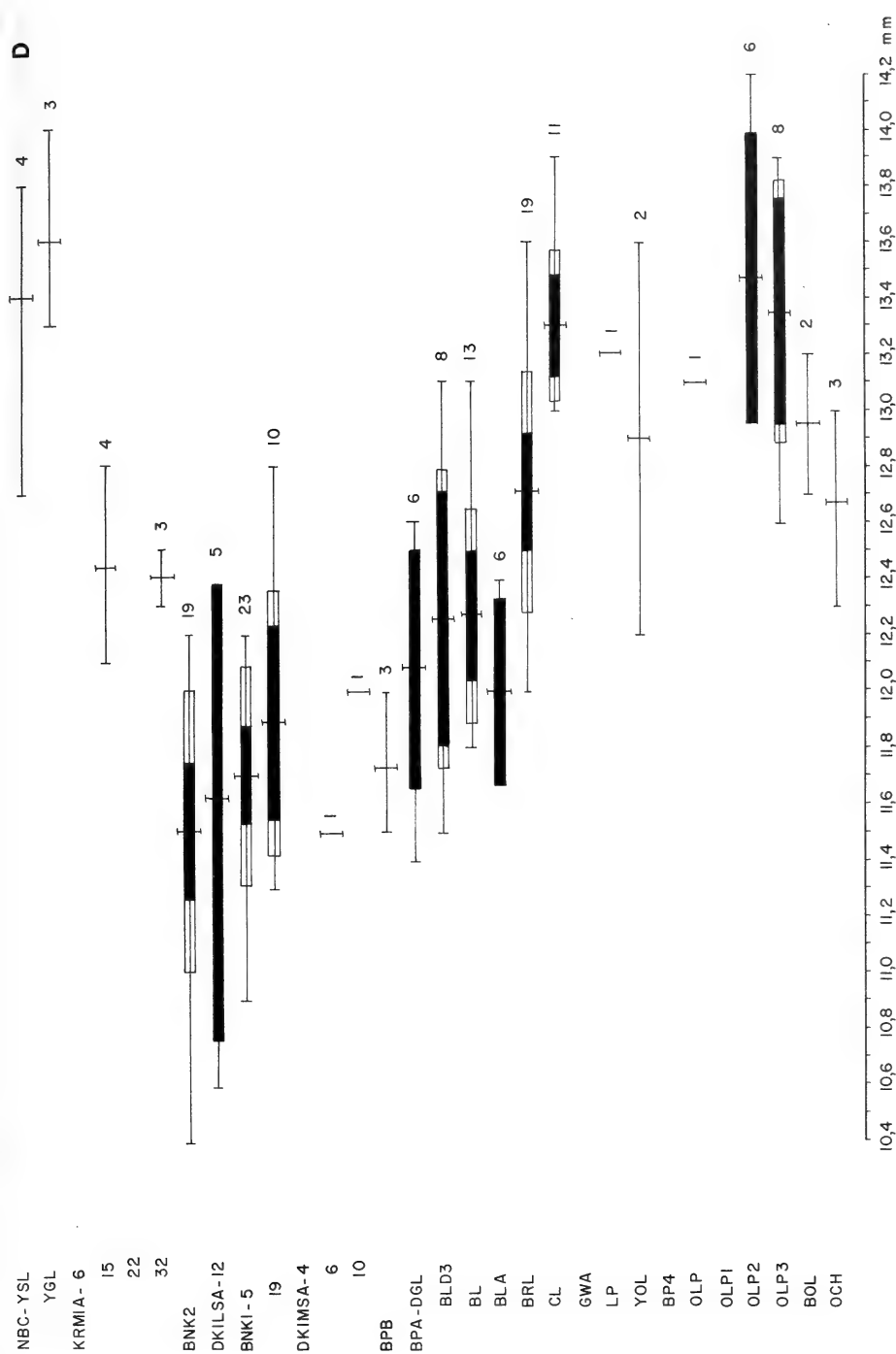


Fig. 17. Variation in parameter C, length of M_{1-3} , in *Crocidura flavescens* from various sites.

the mandible. This parameter has a much higher coefficient of variation (Table 33), presumably because it is affected by the age of the individual. It is therefore much more likely that differences between populations are due, at least in part, to changes in the composition of the population. In other words, if there were a higher proportion of young individuals the mean would be lower than if there were a higher proportion of older individuals. The fact that there is a tendency for the percentage of *C. flavescens* in the sample to be higher when mean depth of mandible is less (Fig. 21) may suggest a population explosion when the proportion of younger individuals was unusually high. On the other hand, the fact that changes are mirrored, albeit less obviously, in the



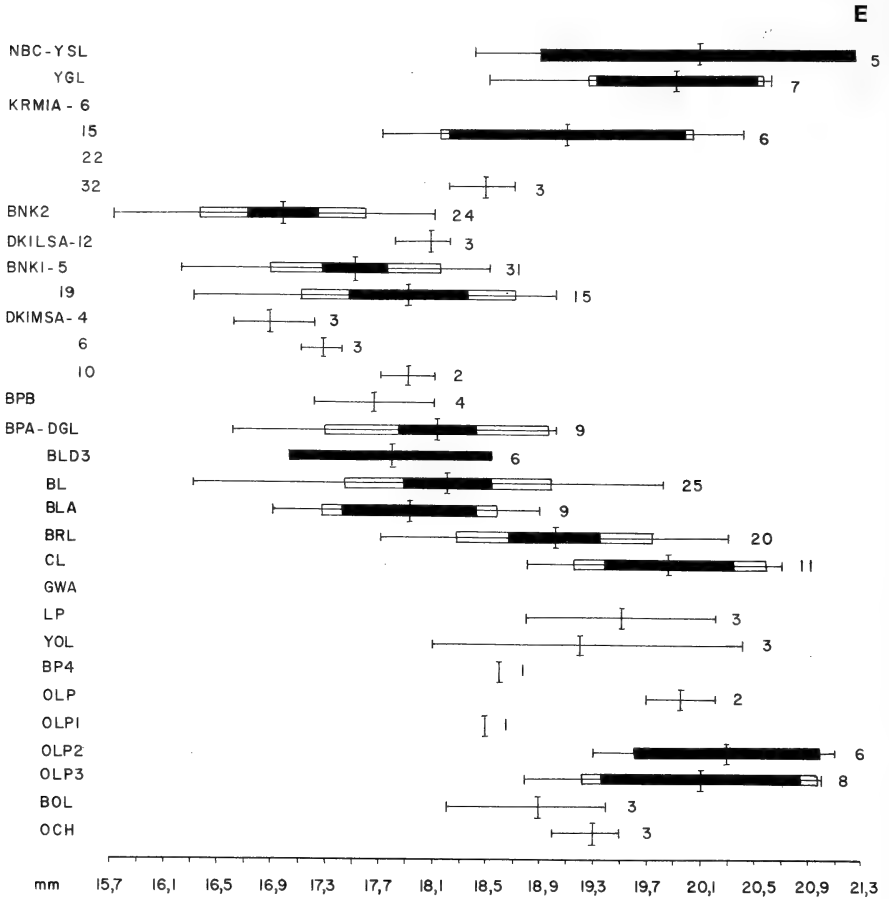


Fig. 19. Variation in parameter E, length of mandible plus incisor, in *Crocidura flavescens* from various sites.

other parameters, indicates real change must also have been taking place. In particular, the length of M_{1-3} , which has low coefficients of variation (Table 33), shows this to be the case. Of some interest, within the fluctuations, is the fact that levels DGL1 and DGL2 indicate a reverse trend which suggests a cooler period at the top of the sequence.

In general, the differences between means of one population and those of preceding or succeeding populations are not statistically significant. This would suggest that the rate of change was normally relatively slow. On at least two occasions, however, there would appear to have been an increase in the rate of change. Given the one-sided hypothesis that successively younger levels in the postglacial period should contain populations of smaller individuals, the differences between levels BRL6 and BRL5, and levels BLD3 and BLD2A are significant (Table 34). In both cases this represents quite rapid change over

periods of a few hundred years. In the first case, means for level BRL5 are significantly smaller than those for level BRL6 in height of ascending ramus and depth of mandible but not in length of M_{1-3} . The mean for this parameter is, however, significantly smaller in level BRL2 than in level BRL7, which also constitutes quite rapid change. The means for height of ascending ramus and length of M_{1-3} in level BLD2A are significantly smaller than those in level BRL3, but not for depth of mandible. Similar periods of accelerated change could well occur in the lower levels but their detection must await analysis of more detailed samples.

The data for other sites are meagre but they do tend to confirm the picture provided by Boomplaas A. At Byneskranskop 1, for instance, the means for level 5 are smaller than those for level 19, except in the depth of the mandible. In this parameter the mean for level 5 is very slightly larger than that for level 19 but this is not considered of any great importance because of the relatively high coefficient of variation, as was discussed above. The means for all parameters in the modern sample from Byneskranskop 2 are considerably smaller than in either of the subfossil samples. The samples from Die Kelders 1 are generally very small and the impression is that the M.S.A. levels are more nearly comparable to the BNK2 sample than the BNK1 samples. The means for

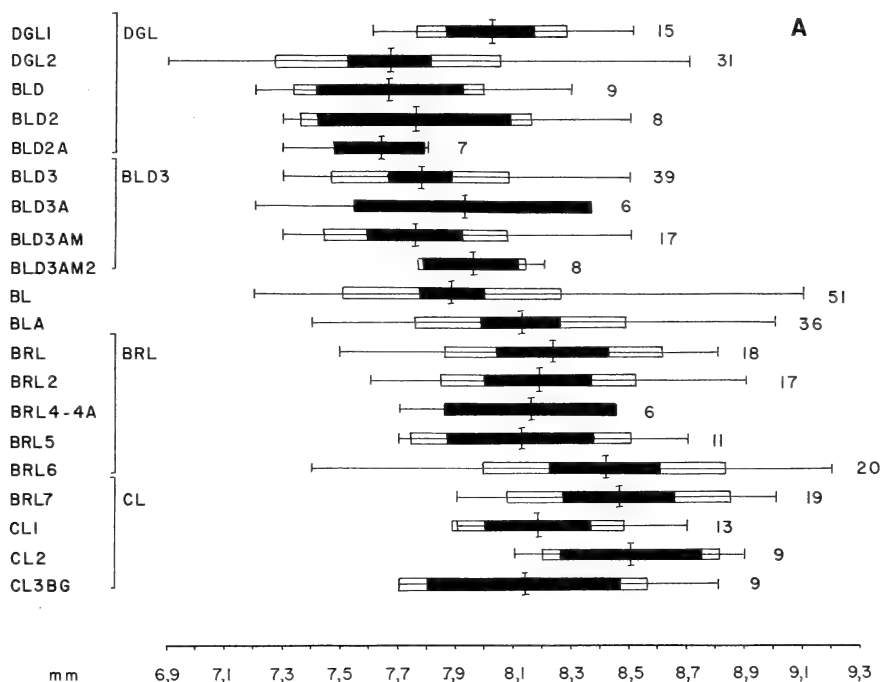


Fig. 20. Variation in parameter A, height of ascending ramus, in *Crocidura flavescens* from postglacial levels at Boomplaas A.

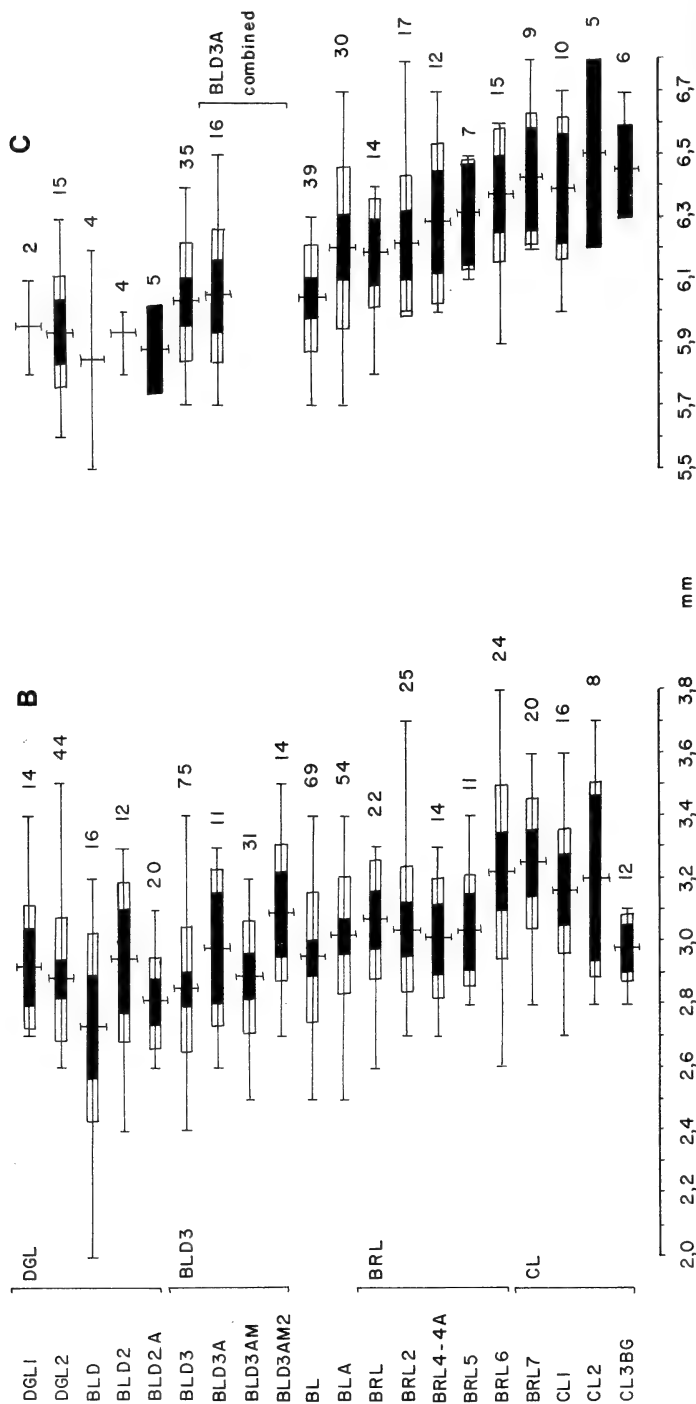


Fig. 21. Variation in parameter B, depth of mandible, and parameter C, length of M_{1.3}, in *Crocidura flavescens* from postglacial levels at Boomplaas A.

TABLE 33

Mean coefficients of variation in parameters measured in *Crocidura flavescens*, *Myosorex varius*, *Aethomys namaquensis*, *Tatera afra*, and *Cryptomys hottentotus*.

	A	B	C	D	E
<i>C. flavescens</i>	4,51	6,61	3,44	3,54	3,90
<i>M. varius</i>	3,33	2,61	3,27	2,87	
<i>A. namaquensis</i>	3,24	3,58	8,67		
<i>T. afra</i>	3,08	3,17			
<i>C. hottentotus</i>	4,90	4,65	8,06	11,84	10,91

See Tables 30 and 36–38 for details of parameters and basic data.

TABLE 34

Selected 't' tests for *Crocidura flavescens*.

	't'	d.f.	P(1-sided)
BPA: BLD3/BLD2A			
A*	3,15	44	0,005–0,0005
B	0,83	93	n.s.
C	1,71	38	0,05
BPA: BRL7/BRL2			
C	2,35	24	0,025
BPA: BRL6/BRL5			
A	1,90	29	0,025
B	2,06	33	0,025
C	0,63	20	n.s.

* See Table 30 for explanation of parameters and data on which the 't' tests were based.

the L.S.A. level, on the other hand, are higher than any for Byneskranskop or other DK1 levels. It would appear that the M.S.A. levels were deposited during a relatively warm period, but that about 2 000 B.P. (L.S.A. level 12) the area was colder. The samples from Klasies River Mouth 1A show a gradual increase in the means for the various parameters from earlier to later. This is consistent with the apparent pre-Last Glacial age of these deposits. Moreover, levels 9 and 6 have provided means for the non-dental parameters which are even larger than those from Nelson Bay Cave. This is surprising in view of the fact that the two NBC levels were deposited during the last glacial maximum and the means for the parameters are comparable to the greatest at BPA. This would suggest that conditions were already cold in the upper part of the KRM1A sequence, although larger samples are needed before the situation can be verified.

Since the original hypothesis was that geographically separated contemporary populations may vary in mean size of individuals, it follows that a similar situation is likely to have pertained in the past. It also draws attention to the fact that evidence concerning temperature is restricted in its application. It may

TABLE 35

Percentage difference between selected populations of *Crocidura flavescens* and *Myosorex varius* at Boomplaas, Byneskranskop, and Nelson Bay Cave.

<i>C. flavescens</i>					
	BPB/BNK2	BPA: BL/BNK1:5	BPA: CL1/BNK1:19	BPA: LP/NBC:YGL	BPA: GWA/NBC:YSL
A*	5,62	4,51	5,55	2,44	0,24
B	7,28	4,24	12,46	2,86	1,25
C	4,07	4,50	8,86	2,34	1,55
D	2,00	4,87	11,35		
E	3,90	3,95	9,61		
\bar{X}	4,57	4,41	9,57	2,55	1,01
<i>M. varius</i>					
	BPB/BPA: CL1	BNK2/BNK1: 19	BPB/BPA: BL	BNK2/BNK1: 5	
A	6,23	6,31	2,34	3,43	
B	12,86	7,66	5,36	8,43	
C	8,67	3,89	2,72	2,30	
D	12,87	3,89	4,60	1,74	
E	11,33	5,54	3,20	-3,05	
\bar{X}	10,39	5,36	3,64	2,57	
<i>M. varius</i>					
	BPB/BNK2	BPA:BL/BNK1: 5			
A	4,67	7,32			
B	6,63	3,10			
C	4,19	1,69			
\bar{X}	4,50	4,04			

* See Tables 30 and 36 for details of parameters and basic data.

be possible to extrapolate on the basis of known present-day differences. The evidence tends to suggest, however, that the relationship has not been static in the past, which would make such extrapolation potentially misleading. Comparison between approximately contemporary levels at Boomplaas A and Byneskranskop 1 and at Boomplaas A and Nelson Bay Cave illustrates the point (Table 35). It is noticeable that on average the means for Boomplaas A are 9,57 per cent higher than those for BNK1 in the early postglacial period. By about 4 000 B.P. the BPA means are only 4,41 per cent higher. Thereafter, the position appears to have stabilized because the average for the modern BPB sample is virtually the same at 4,57 per cent higher than that for BNK2. With BPA and NBC the situation is not so clear, possibly because of small samples or because the levels cannot be closely correlated or because both were inland sites at the time. However, although the difference between BPA and NBC is much smaller than that between BPA and BNK1, the same point is evident; the percentage difference is not consistent throughout. The present evidence suggests that the climate was relatively either much cooler or more extreme in the Congo valley than around Byneskranskop about 12 000 years ago than it is today. This is indicated not only by the greater difference between the two older levels, but also by the fact that in the Congo valley the BPA level CL1 population is on average 10,39 per cent larger than the BPB population (Table 35). This contrasts with Byneskranskop where the BNK1 level 19 population is on average only 5,36 per cent larger than the BNK2 population. Even such initial exercises illustrate the potential of such work for providing detailed regional climatic information.

Myosorex varius

Four parameters were measured in *Myosorex varius* as was described above. Table 36 gives the data for the different populations and these are

TABLE 36
Size variation in mandibles of *Myosorex varius*.

	A: height of ascending ramus					B: length of mandible plus incisor					C: length of lower tooth row					D: length of P ₄ to M ₃					
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	
BPA: DGL	.	37	5.0-5.7	5.39	0.17	0.06	9	12.8-13.4	13.09	0.18	0.14	8	7.5-8.6	8.43	0.29	0.24	10	5.0-5.7	5.54	0.20	0.14
BLD3	.	26	5.1-5.6	5.37	0.14	0.06	7	12.1-13.2	12.83	0.42	0.38	5	7.5-8.4	7.98	0.41	0.51	16	5.0-5.9	5.56	0.23	0.12
BL	.	21	5.0-5.7	5.33	0.18	0.08	17	12.2-13.6	12.89	0.37	0.19	9	7.8-8.4	8.26	0.19	0.15	16	5.4-5.9	5.60	0.16	0.08
BLA	.	11	5.3-5.6	5.46	0.09	0.06	1 (12.6)					2 (8.3)				5	5.4-5.6	5.54	0.09	0.11	
BRL	.	38	5.0-6.0	5.29	0.23	0.08	8	11.9-13.2	12.38	0.42	0.35	3	7.9-8.4	8.20			26	5.1-5.6	5.37	0.14	0.06
CL	.	37	4.9-5.6	5.18	0.18	0.06	15	12.0-13.2	12.53	0.35	0.20	11	7.6-8.4	7.89	0.27	0.18	29	5.0-5.7	5.33	0.17	0.06
GWA	.	30	5.0-5.5	5.29	0.13	0.05	3	12.4-13.3	12.73			2 (8.0)				21	5.2-5.7	5.45	0.16	0.07	
LP	.	42	4.9-5.7	5.29	0.17	0.05	3	12.1-13.1	12.50			2	7.8-8.0	7.90			50	5.1-5.7	5.40	0.14	0.04
LPC	.	19	5.0-6.1	5.28	0.29	0.14						1 (8.0)				12	5.3-5.7	5.46	0.16	0.10	
YOL	.	20	5.1-5.7	5.34	0.24	0.11	8	12.0-12.8	12.56	0.30	0.25	5	8.0-8.3	8.12	0.30	0.16	21	5.2-5.8	5.53	0.16	0.07
BPI	.	27	4.9-5.5	5.31	0.19	0.08	5	11.8-12.4	12.10	0.28	0.35	7	7.1-8.2	7.76	0.34	0.13	25	5.2-5.7	5.43	0.14	0.06
BP4	.	52	4.9-5.6	5.21	0.17	0.05	9	11.0-12.7	12.10	0.51	0.39	5	7.5-8.2	7.86	0.26	0.32	28	5.0-5.6	5.28	0.15	0.03
OLP	.	23	4.9-5.6	5.22	0.17	0.08	6	11.7-13.0	12.28	0.44	0.46	4	7.6-8.2	7.80			11	5.1-5.9	5.39	0.24	0.16
OLP1	.	36	5.0-5.6	5.33	0.17	0.06	12	11.9-12.8	12.41	0.27	0.17	7	7.4-8.1	7.83	0.26	0.24	36	5.1-5.7	5.45	0.16	0.05
OLP2	.	39	4.9-5.6	5.31	0.18	0.06	55	11.9-13.2	12.66	0.30	0.08	36	7.6-8.6	8.11	0.23	0.08	41	5.2-5.8	5.51	0.15	0.05
OLP3	.	32	4.8-5.7	5.30	0.19	0.07	41	11.8-13.3	12.60	0.32	0.10	25	7.4-8.5	8.14	0.33	0.14	44	5.1-5.8	5.50	0.15	0.05
BOL	.	34	4.9-5.6	5.33	0.22	0.08	21	12.1-13.2	12.61	0.30	0.14	14	7.9-8.5	8.09	0.18	0.10	33	5.1-5.8	5.45	0.16	0.06
BOL4/5	.	21	4.9-5.5	5.33	0.19	0.09	2	12.7-13.0	12.85			3	8.2-8.5	8.33			8	5.5-5.7	5.59	0.06	0.05
OCH	.	40	5.2-5.7	5.42	0.14	0.05	14	12.6-13.7	12.96	0.34	0.20	8	8.1-8.7	8.36	0.23	0.19	45	5.3-6.0	5.61	0.14	0.04
LOH	.	20	5.2-5.7	5.45	0.18	0.08	2	12.7-13.2	12.95			2	7.8-8.6	8.20			10	5.3-5.8	5.57	0.16	0.11
BNK1: 5	.	45	5.4-6.2	5.72	0.16	0.05	44	12.4-13.9	13.29	0.28	0.08	22	7.4-8.8	8.40	0.31	0.14	34	5.2-6.0	5.73	0.16	0.06
DK1: L.S.A.12	.	25	5.4-6.1	5.75	0.18	0.13	22	12.8-14.3	13.38	0.28	0.13	10	8.1-9.2	8.54	0.30	0.21	12	5.3-6.2	5.78	0.25	0.16
M.S.A.4	.	46	5.5-6.4	5.76	0.18	0.05	35	13.1-14.1	13.57	0.26	0.09	9	8.4-9.0	8.71	0.20	0.16	27	5.6-6.1	5.83	0.17	0.07
8	.	28	5.6-6.3	5.85	0.18	0.07	18	12.9-14.3	13.68	0.41	0.20	5	8.4-9.1	8.88	0.28	0.34	23	5.6-6.2	5.87	0.15	0.07
11	.	66	5.3-6.4	5.86	0.21	0.05	54	13.0-14.2	13.65	0.31	0.09	14	8.4-8.9	8.69	0.17	0.10	23	5.6-6.1	5.84	0.13	0.06
BPB	.	33	4.8-5.6	5.35	0.19	0.07	36	12.3-13.4	12.74	0.34	0.11	32	7.5-8.6	8.12	0.25	0.09	39	5.2-5.8	5.51	0.15	0.05
BNK2	.	49	5.3-6.1	5.60	0.16	0.05	68	12.8-14.0	13.33	0.35	0.09	55	7.6-8.9	8.46	0.30	0.08	63	5.4-6.1	5.72	0.16	0.04
NGB	.	56	5.0-5.7	5.35	0.16	0.04	68	12.3-13.4	12.73	0.31	0.07	40	7.7-8.6	8.12	0.25	0.08	49	5.2-5.8	5.49	0.16	0.05

95%=95% confidence interval for the mean.

Measurements in mm.

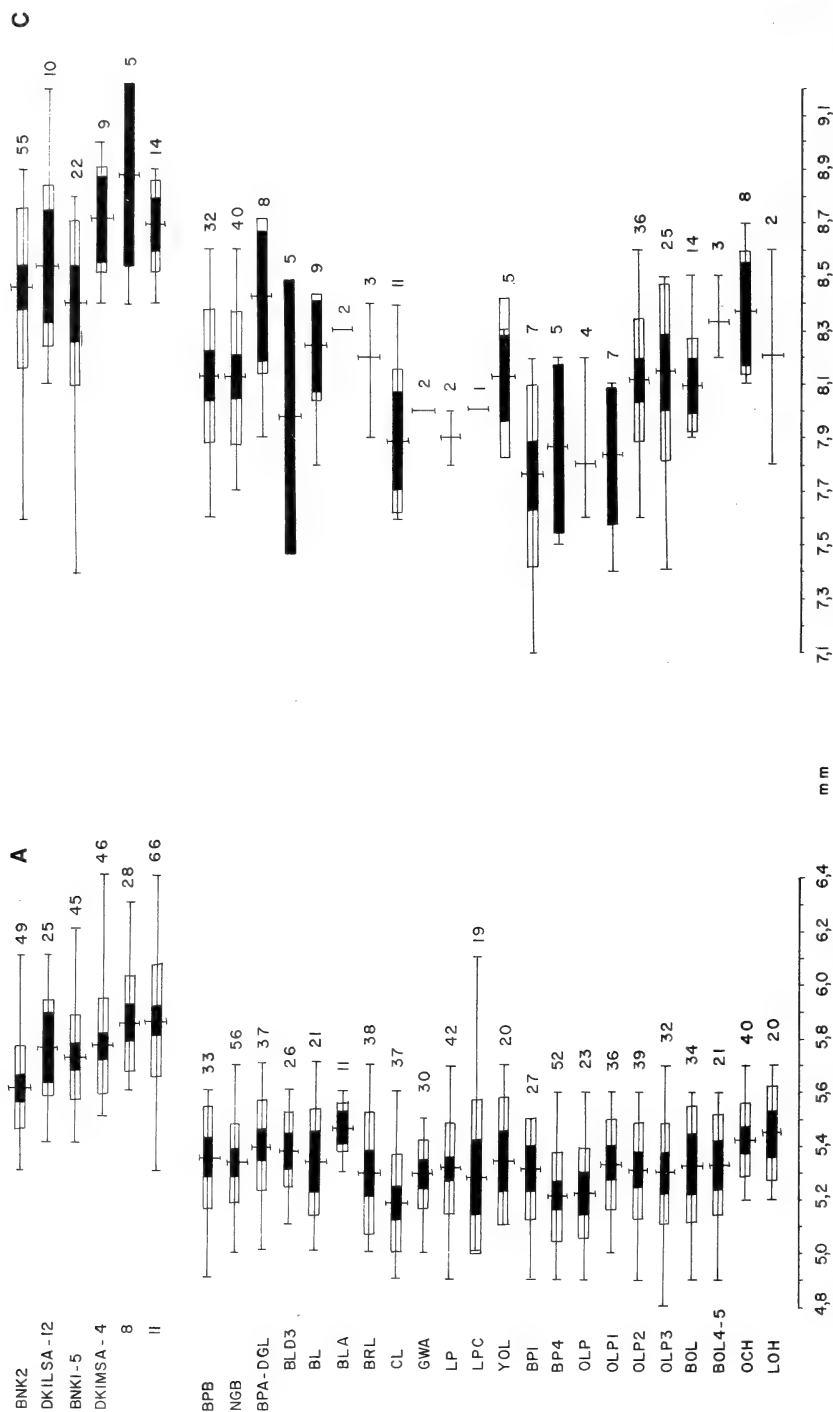


Fig. 22. Variation in parameter A, height of ascending ramus, and parameter C, length of lower tooth row, in *Myosorex varius* from various sites.

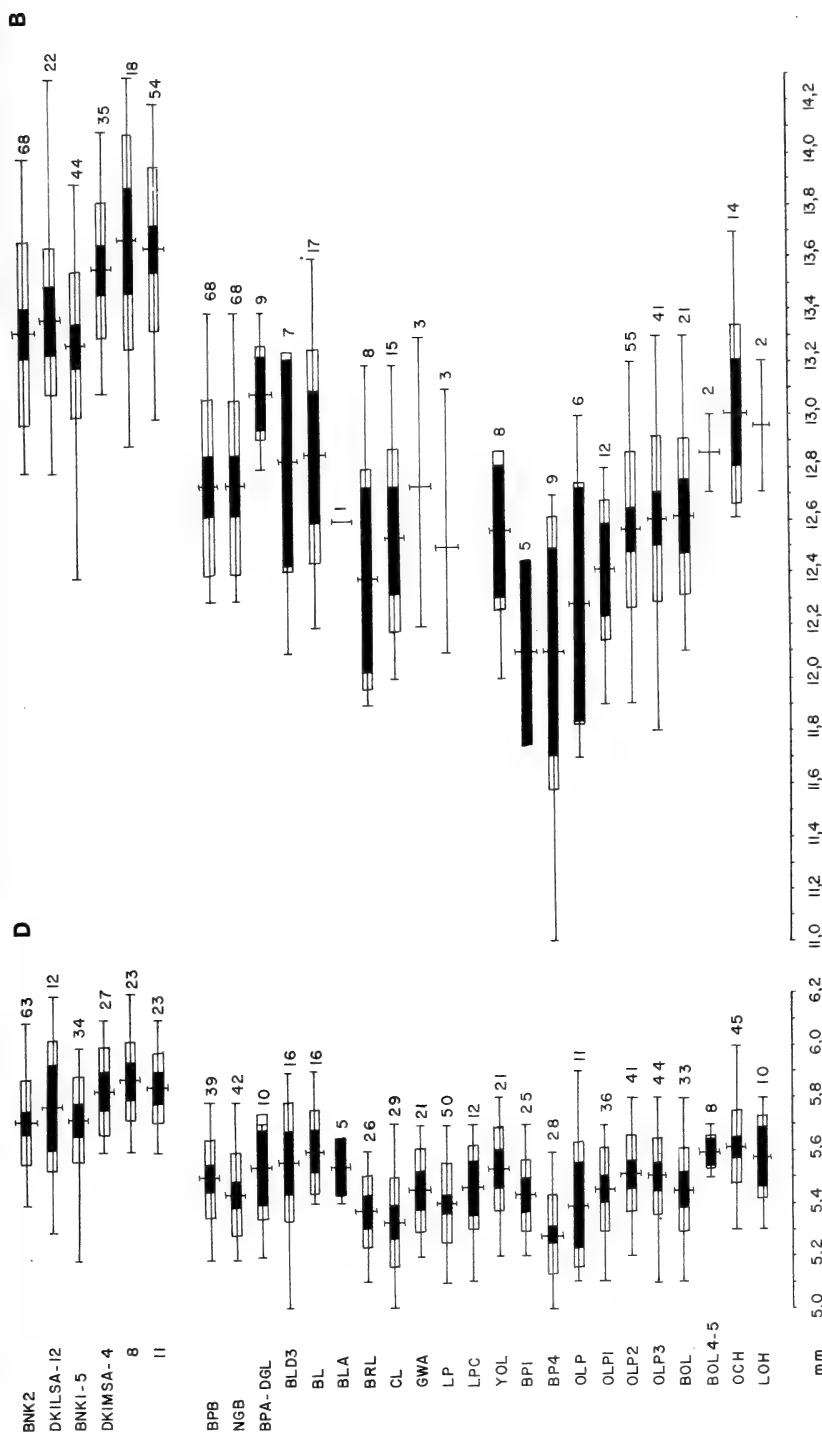


Fig. 23. Variation in parameter B, length of mandible plus incisor, and parameter D, length of P_4-M_3 , in *Myosorex varius* from various sites.

shown graphically in Figures 22–23. In Figure 15 variation in the means for the different parameters in the Boomplaas A sequence is plotted. As with *Crociodura flavescens*, there is considerable variation, with the pattern being clearest in the sequence from Boomplaas A.

The pattern of change is very similar in all parameters. This is not unexpected since three of the parameters were, in effect, alternatives. For this reason the best represented, length of P_4 to M_3 , will be taken as representative of the three length measurements in the following discussion. The coefficients of variation for this parameter are low and are only moderate for height of ascending ramus (Table 33). It would seem, therefore, on arguments put forward above, that real change in the mean size of individuals is being monitored. This change would appear to have been generally gradual; certainly there are as yet no demonstrable periods of accelerated change, although these may be found in the lower levels later.

There are several major trends noticeable in the Boomplaas A sequence. From the base there is a general decline in mean size for the various parameters until level BP4. Thereafter, a moderate increase in levels BP1 and YOL leads eventually to a decline culminating in level CL. A general increase in the early postglacial period is replaced in level BLA or BL by a slight decrease. As a generality most of the Holocene levels contain populations whose mean mandible size is larger than those in most of the Upper Pleistocene populations. This would suggest that *Myosorex varius* displays a negative response to Bergmann's Rule. If this were the case, the evidence would suggest that temperatures in the lowermost levels were comparable to those of the Holocene. By the same token, the coldest periods in the sequence would be in levels OLP–BP4 and again in level CL. This picture is not entirely in accordance with that suggested by other lines of evidence and it may be that there is some other explanation for the size variation. Possibly rainfall or effective precipitation may play a part in determining the size of individuals. It is, however, also possible that the apparent anomalies may be due to lack of information and that when more complete data are available the situation will be clarified. The limited data from other sites indicate that this is perhaps most likely since results vary inversely to those obtained for *Crociodura flavescens*. Table 35 shows that the percentage difference in mean size of individuals in contemporary samples from Boomplaas and Byneskranskop is virtually identical to that found in *C. flavescens*. However, *Myosorex varius* is smaller inland than on the coast, whereas the reverse is true for *Crociodura flavescens*. The Die Kelders 1 M.S.A. levels show a reduction from earlier to later mean individual size, with no change in the L.S.A. sample. This is not the complete reverse of the situation in *C. flavescens*, although it tends to hold good in the M.S.A. sample. Larger samples of *C. flavescens* would almost certainly have clarified the situation. It seems in general, therefore, that the size of the *Myosorex varius* will be shown to vary in response to changing temperature, but in contradiction to Bergmann's Rule.

Aethomys namaquensis and *Tatera afra*

Aethomys namaquensis was measured in three parameters and *Tatera afra* in two, as was described above. Tables 37 and 38 give the data on size variation in these two species and Figures 24 and 26 show these data graphically. Figure 25 illustrates variation in the means of different parameters for *A. namaquensis* at Boomplaas A. The mean coefficients of variation for dental parameters are fairly low in both species, but depth of mandible in *A. namaquensis* is very much higher (Table 33). This is probably due to the fact that this parameter is likely to be influenced by the age of the individual and possibly the sex as well. The size of the teeth, on the other hand, is apparently little affected by either of these factors.

TABLE 37

Size variation in teeth and depth of mandible in *Aethomys namaquensis* from the Congo valley.

A: length of M ¹⁻³						B: length of M ₁₋₃					C: depth of body of mandible				
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
BPA: DGL .	23	5,1-5,8	5,49	0,19	0,08	27	5,1-5,7	5,38	0,20	0,08	43	3,1-4,5	3,77	0,34	0,10
BLD3 .	26	5,2-5,9	5,56	0,18	0,07	34	5,0-6,0	5,45	0,17	0,06	34	3,0-4,3	3,79	0,34	0,12
BL .	19	5,4-6,0	5,64	0,17	0,08	31	5,1-5,9	5,53	0,17	0,06	31	3,2-4,8	3,90	0,32	0,12
BLA .	14	5,3-5,9	5,57	0,17	0,10	11	5,3-5,7	5,47	0,18	0,12	8	3,6-4,6	4,11	0,29	0,24
BRL .	136	5,1-6,0	5,60	0,16	0,03	88	5,1-6,0	5,54	0,18	0,04	83	3,0-4,5	3,88	0,34	0,07
CL .	30	5,2-6,1	5,65	0,20	0,07	23	5,3-5,8	5,57	0,16	0,07	28	3,4-4,6	3,94	0,28	0,11
LP .	5	5,5-5,9	5,74	0,17	0,21	1	(5,7)				5	3,0-3,8	3,40	0,40	0,50
BP4 .	6	5,5-5,9	5,75	0,16	0,17	5	5,1-5,8	5,52	0,30	0,38	10	3,3-4,3	3,75	0,27	0,19
OLP1 .	5	5,6-6,1	5,90	0,20	0,25	9	5,4-5,8	5,60	0,13	0,10	12	2,8-4,1	3,63	0,41	0,26
OLP2 .	36	5,5-6,4	5,86	0,21	0,07	33	5,4-6,0	5,72	0,16	0,06	35	3,0-4,7	3,82	0,39	0,13
OLP3 .	34	5,6-6,4	5,94	0,20	0,07	28	5,4-6,0	5,64	0,17	0,07	30	2,8-4,4	3,70	0,44	0,16
BOL .	4	5,8-6,2	6,03			6	5,5-6,1	5,80	0,26	0,27	10	3,7-4,3	4,03	0,21	0,15
NGB . . .	17	5,1-5,9	5,51	0,20	0,10	18	4,7-5,8	5,32	0,30	0,15	18	3,3-4,2	3,82	0,23	0,12

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 38

Size variation in teeth of *Tatera afra*.

A: length of M ₁₋₂						B: length of M ¹⁻²				
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
BNK1: 5	9	5,0-5,2	5,09	0,09	0,07	3	4,7-4,8	4,77		
19	5	5,0-5,5	5,28	0,22	0,27	4	5,1-5,6	5,30		
BNK2	18	4,7-5,3	4,99	0,16	0,08	7	4,6-5,2	4,96	0,19	0,18
DK1MSA: 1	3	(5,2)				6	4,8-5,2	5,00	0,13	0,13
3	18	4,8-5,2	5,04	0,15	0,08	19	4,8-5,3	4,95	0,15	0,07
5	22	4,8-5,4	5,13	0,16	0,07	38	4,7-5,3	4,93	0,15	0,05
7	29	4,8-5,3	5,13	0,12	0,05	34	4,6-5,3	4,91	0,17	0,06
9	10	5,0-5,4	5,22	0,15	0,11	14	4,5-5,1	4,88	0,20	0,12
11	9	4,8-5,4	5,09	0,16	0,12	18	4,7-5,1	4,92	0,12	0,06
13	1	(4,9)				3	4,9-5,3	5,10		
NBC: YSL Δ 3-5	38	5,3-6,0	5,63	0,19	0,06	48	5,1-5,7	5,43	0,14	0,04
YGL β 1-4	31	5,2-6,3	5,76	0,22	0,08	48	4,9-5,9	5,46	0,19	0,05

Measurements in mm.

95% = 95% confidence interval for the mean.

It is unfortunate that samples of *A. namaquensis* are available only from the Congo valley and of *T. afra* only from the coastal sites. For this reason it has not been possible to check possible trends in contemporary sites. It would appear, however, that in *A. namaquensis* there is a general reduction in the size of the teeth from the earliest levels at Boomplaas A to the latest; the mean size of the teeth in the Nooitgedacht B sample is also low (Figs 24–25). This trend does not seem to be correlated with temperature change and, as such, is of little value in the present context, although it is almost certainly of intrinsic interest. The depth of the mandible in *A. namaquensis* provides a very clear pattern (Figs. 24–25) which suggests that, like *M. varius*, this species may respond negatively to Bergmann's Rule. In this parameter the mean size in postglacial populations is noticeably larger in most cases than it is in the glacial populations.

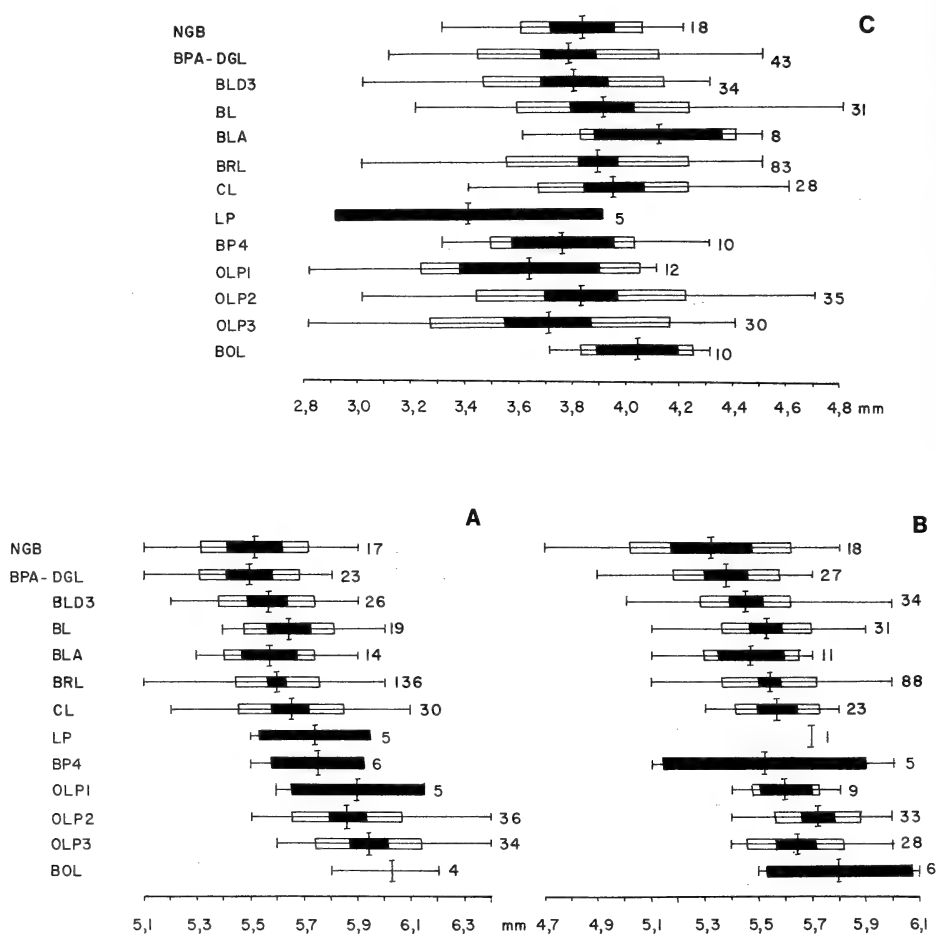
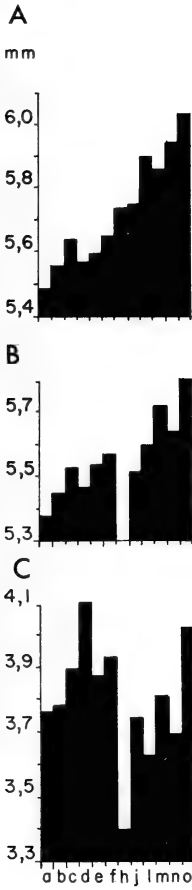


Fig. 24. Variation in parameter A, length of M_{1-3} , parameter B, length of M_{1-3} , and parameter C, depth of mandible, in *Aethomys namaquensis* from the Congo Valley.

a	DGL	o	BOL
b	BLD3	p	OCH
c	BL	al	DGL1
d	BLA	a2	DGL2
e	BRL	a3	BLD2
f	CL	a4	BLD2A
g	GWA	el	BRL
h	LP	e2	BRL2
i	YOL	e3	BRL4
j	BP4	e4	BRL5
k	OLP	e5	BRL6
l	OLP1	f1	BRL7
m	OLP2	f2	CL1
n	OLP3	f3	CL3BG

A.namaquensis



C.hottentotus

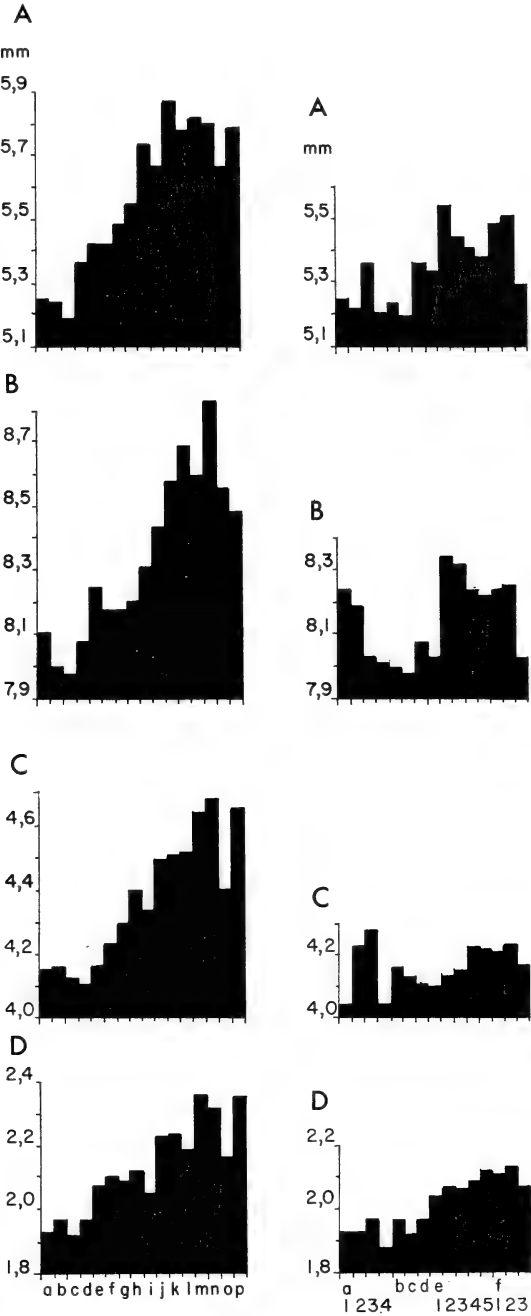


Fig. 25. Variation in means of parameters measured in *Cryptomys hottentotus* and *Aethomys namaquensis* from Boomplaas A. See Tables 37, 39–40 for details.

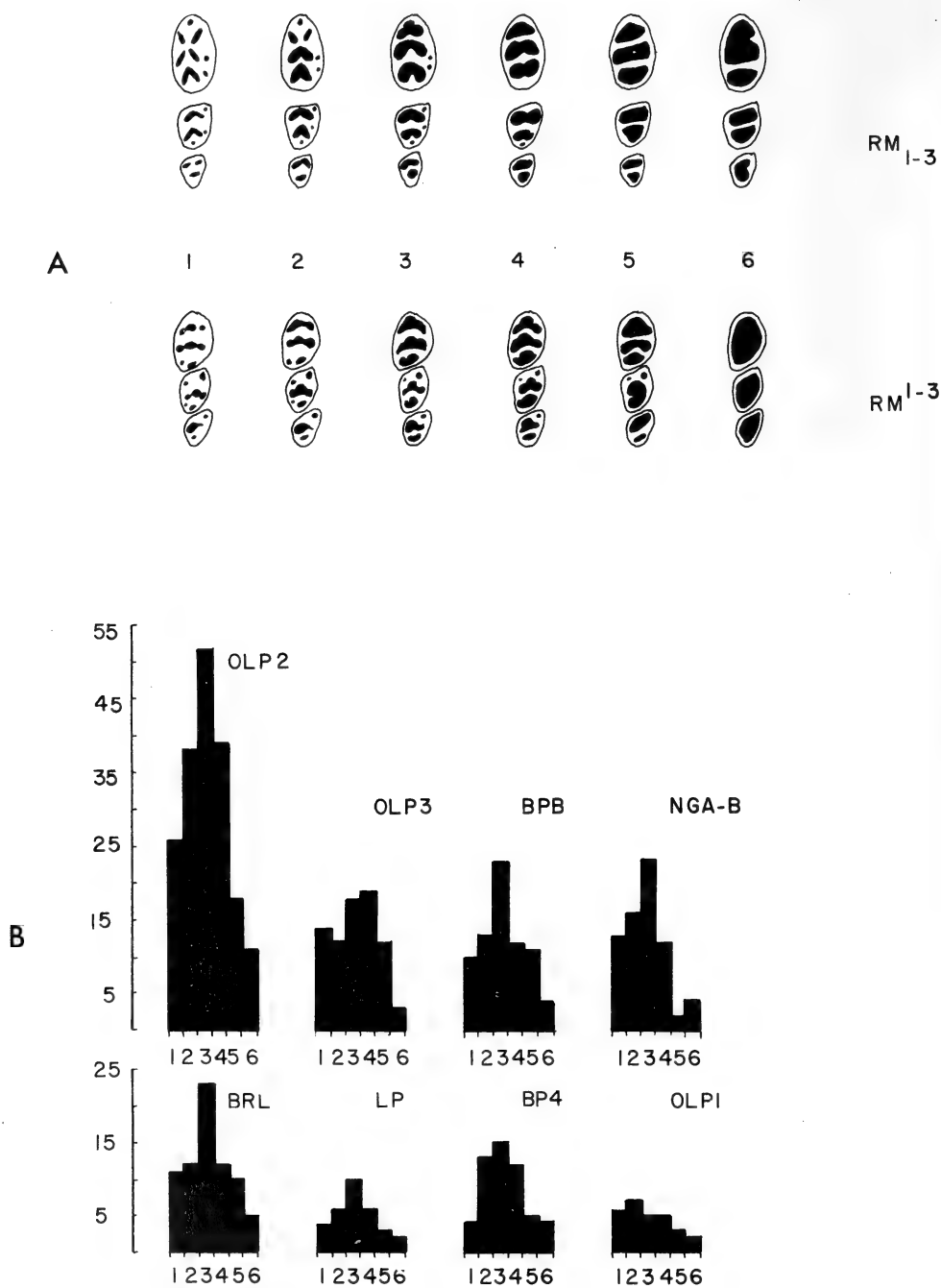


Fig. 26. A. Tooth-wear categories in *Aethomys namaquensis*. B. Numbers of individuals in each category in selected samples from the Congo Valley.

An interesting fact is that the coefficients of variation vary inversely with mean depth of mandible (Fig. 25). Thus, when the depth of mandible is great the coefficient of variation is low, and vice versa. This suggests that there is some connection between the two. One possibility was that there were changes in the age composition of the populations at different times as was suggested for *Crocidura flavescens*. It may be, for instance, that in Boomplaas A level BLA the population sample consisted of mostly mature or older individuals with few young individuals, which would give a relatively high mean depth of mandible and a relatively low coefficient of variation. In level LP, on the other hand, the age groups may be much more evenly represented but with the emphasis on younger individuals. A pilot study was undertaken in which the samples were divided into six age categories based on the degree of tooth wear (Fig. 26) such as was done by Davis (1959) and Dean (1973) for *Praomys natalensis*. This showed that there were apparently no clear-cut differences in the composition of the samples (Fig. 26). The general proportions were similar in all the samples examined and the extent of the observed range in individual size variation was also similar for all levels (Table 37). This latter fact would suggest that neither the young nor the old were missing from the samples. It may be that with more data a pattern would emerge, but present evidence does not suggest that there exist differences in proportions of age categories such as could explain the observed pattern. It will, however, probably be worth examining this problem in greater detail in order to establish what mechanisms may be operating as well as what environmental information is forthcoming.

For *Tatera afra* the evidence from Die Kelders 1 is not internally consistent. That is to say, the data from the upper teeth do not exhibit the same trends as do the lower teeth (Fig. 27). It is difficult to know how this may be interpreted but it seems unlikely that it can have any environmental significance. It also means that it is not possible, on present evidence, to decide which set of data may be more reliable for palaeoenvironmental interpretation. The fact that the general relationship between samples from Die Kelders 1, Byneskranskop 1 and Nelson Bay Cave is similar to that found in *Crocidura flavescens*, would suggest that there may be some potential information to be gained from *T. afra*. It looks as if *T. afra* is conforming to Bergmann's Rule, but more data are needed before this can be confirmed or refuted.

Cryptomys hottentotus

Mandibles of *Cryptomys hottentotus* from Boomplaas A and B-C were measured in five parameters as was described above. The resulting data are given in Tables 39 and 40 and these results are shown graphically in Figures 28-30. Figure 25 illustrates variation in the mean for the various parameters. The mean coefficients of variation indicate that alveolar length and distance between posterior border of M₃ and posterior border of symphysis are apparently little affected by age or sex (Table 33). There is much more

TABLE 39

Size variation in mandibles of *Cryptomys hottentotus* from Boomplaas.

	A: alveolar length					B: posterior border M ₃ -symph				
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	
BPA: DGL	60	4,5-6,1	5,25	0,31	0,08	60	7,3-9,1	8,11	0,4	
BLD3	30	4,9-5,8	5,24	0,25	0,09	30	7,3-9,3	8,00	0,4	
BL	30	4,7-5,6	5,19	0,22	0,08	30	7,5-8,8	7,98	0,3	
BLA	30	4,7-5,8	5,37	0,29	0,11	30	7,5-8,7	8,08	0,3	
BRL	121	4,9-6,1	5,43	0,26	0,05	121	7,3-9,1	8,25	0,4	
CL	90	4,8-6,2	5,43	0,26	0,05	90	7,3-9,3	8,18	0,4	
GWA	30	5,0-5,8	5,49	0,27	0,10	30	7,5-8,7	8,18	0,3	
LP	30	4,9-6,2	5,55	0,32	0,12	30	7,3-8,8	8,21	0,3	
YOL	10	5,3-6,0	5,74	0,19	0,14	10	7,9-8,9	8,31	0,3	
BP4	30	5,1-6,3	5,67	0,29	0,11	30	7,9-9,3	8,44	0,3	
OLP	14	5,4-6,4	5,87	0,32	0,19	14	8,0-9,4	8,58	0,4	
OLP1	30	5,2-6,2	5,78	0,29	0,11	30	7,5-9,7	8,69	0,5	
OLP2	30	5,3-6,4	5,82	0,26	0,10	30	7,8-9,2	8,60	0,4	
OLP3	30	5,2-6,1	5,80	0,24	0,09	30	8,3-9,4	8,83	0,2	
BOL	30	5,3-6,3	5,67	0,28	0,10	30	7,8-9,4	8,56	0,4	
OCH	30	5,2-6,3	5,79	0,31	0,12	30	7,8-9,2	8,49	0,4	
BPB-C	16	4,8-5,4	5,21	0,18	0,10	16	7,8-8,8	8,29	0,3	

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 40

Size variation in mandibles of *Cryptomys hottentotus* from Boomplaas A upper levels.

	A: Alveolar length					B: posterior border M ₃ -symph				
	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	
Unit DGL										
DGL1	10	4,8-5,7	5,25	0,28	0,20	10	7,9-8,8	8,24	0,34	
DGL2	20	4,5-5,9	5,22	0,30	0,14	20	7,5-9,0	8,19	0,38	
BLD2	13	4,8-6,1	5,36	0,39	0,23	13	7,3-9,1	8,03	0,50	
BLD2A	17	4,9-5,7	5,21	0,26	0,13	17	7,3-8,8	8,01	0,41	
Unit BRL										
BRL	12	5,0-5,8	5,34	0,23	0,15	12	7,3-8,5	8,03	0,40	
BRL2	19	5,2-6,1	5,55	0,29	0,14	19	7,5-9,0	8,35	0,39	
BRL4	30	5,0-6,0	5,45	0,26	0,10	30	7,5-9,0	8,32	0,42	
BRL5	30	4,9-6,1	5,42	0,28	0,10	30	7,3-9,1	8,24	0,47	
BRL6	30	4,9-5,8	5,39	0,24	0,09	30	7,4-9,0	8,23	0,46	
Unit CL										
BRL7	30	4,8-6,0	5,49	0,27	0,10	30	7,5-9,3	8,25	0,45	
CL1	30	5,1-6,2	5,52	0,26	0,10	30	7,8-9,2	8,26	0,37	
CL3BG	30	4,9-5,6	5,30	0,19	0,07	30	7,3-8,6	8,03	0,33	

Measurements in mm.

95% = 95% confidence interval for the mean.

h attachment ascending ramus				D: foramen mentale-alveolar margin					E: depth of mandible				
Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
4-8	4,16	0,35	0,10	60	1,5-2,5	1,93	0,23	0,06	21	4,0-6,0	4,89	0,70	0,32
4-9	4,16	0,33	0,12	30	1,5-2,9	1,97	0,30	0,11	10	3,6-5,8	4,89	0,70	0,55
5-5,5	4,13	0,44	0,16	30	1,5-2,4	1,92	0,25	0,09	7	4,4-6,1	5,07	0,66	0,61
4-9	4,11	0,34	0,13	30	1,5-2,3	1,97	0,22	0,08	1	(5,5)			
4-5,3	4,17	0,36	0,06	121	1,6-2,7	2,08	0,23	0,04	20	4,2-6,4	5,04	0,50	0,23
4-5,2	4,24	0,35	0,07	90	1,7-2,7	2,11	0,21	0,05	31	4,2-6,7	5,15	0,69	0,25
4-5,2	4,30	0,42	0,16	30	1,7-2,6	2,09	0,22	0,08	3	4,6-6,8	5,93		
4-5,1	4,41	0,30	0,11	30	1,7-2,6	2,13	0,24	0,09	3	5,4-6,1	5,67		
4-4,7	4,34	0,23	0,16	10	1,7-2,3	2,05	0,21	0,15	1	(5,0)			
4-5,2	4,50	0,31	0,11	30	1,7-2,8	2,23	0,25	0,09	5	5,2-6,2	5,60	0,39	0,49
4-4,9	4,51	0,34	0,20	14	1,8-2,7	2,24	0,24	0,14					
4-5,8	4,52	0,43	0,16	30	1,6-2,8	2,19	0,30	0,11	11	4,8-6,3	5,50	0,52	0,35
4-5,5	4,64	0,40	0,15	30	1,8-3,1	2,36	0,33	0,12	30	4,6-7,5	5,71	0,67	0,25
4-5,5	4,68	0,31	0,11	30	1,6-3,1	2,32	0,32	0,12	20	4,5-7,2	5,73	0,64	0,30
4-5,0	4,41	0,31	0,12	30	1,7-2,8	2,17	0,25	0,09	14	4,9-6,0	5,49	0,39	0,22
4-6,0	4,66	0,41	0,15	30	1,9-3,0	2,36	0,24	0,09	8	5,0-6,7	5,79	0,60	0,50
4-4,6	4,06	0,34	0,18	16	1,7-2,4	2,03	0,18	0,10	16	4,1-6,8	5,12	0,65	0,35

h attachment ascending ramus				D: foramen mentale-alveolar margin					E: depth of mandible				
Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
4-4,5	4,04	0,39	0,28	10	1,6-2,5	1,93	0,29	0,21	4	4,0-5,6	4,90		
6-4,8	4,23	0,34	0,16	20	1,6-2,3	1,93	0,17	0,08	10	4,0-6,0	4,79	0,79	0,56
5-4,8	4,28	0,38	0,23	13	1,5-2,4	1,97	0,25	0,15	5	4,3-6,0	5,10	0,72	0,89
6-4,6	4,04	0,29	0,15	17	1,5-2,4	1,88	0,25	0,13	2	4,6-5,1	4,85		
5-4,9	4,10	0,39	0,25	12	1,7-2,6	2,04	0,23	0,14	1	(6,4)			
6-4,8	4,13	0,33	0,16	19	1,7-2,4	2,07	0,24	0,11	4	4,2-5,3	4,85		
2-5,0	4,15	0,35	0,13	30	1,6-2,5	2,07	0,24	0,09	8	4,3-5,6	5,03	0,41	0,34
6-5,3	4,22	0,35	0,13	30	1,6-2,5	2,09	0,21	0,08	5	4,3-5,2	4,88	0,41	0,51
5-5,1	4,21	0,39	0,15	30	1,7-2,7	2,12	0,23	0,09	2	5,1-5,2	5,15		
5-5,0	4,29	0,33	0,12	30	1,7-2,6	2,11	0,21	0,08	5	4,5-6,3	5,12	0,71	0,88
6-4,9	4,23	0,30	0,11	30	1,9-2,5	2,13	0,19	0,07	8	4,3-5,5	4,94	0,50	0,42
5-5,2	4,19	0,43	0,16	30	1,7-2,7	2,07	0,25	0,09	18	4,2-6,7	5,26	0,76	0,38

TABLE 39

Size variation in mandibles of *Cryptomys hottentotus* from Boomplaas.

		A: alveolar length					B: posterior border M ₂ -symphysis					C: attachment ascending ramus					D: foramen mentale-alveolar margin					E: depth of mandible				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
BPA-C	DGL	60	4.5-6.1	5.25	0.31	0.08	60	7.3-9.1	8.11	0.41	0.10	14-4.8	4.16	0.35	0.10	60	1.5-2.5	1.93	0.23	0.06	21	4.0-6.0	4.89	0.70	0.32	
	BLD3	30	4.9-5.8	5.24	0.25	0.09	30	7.3-9.3	8.00	0.44	0.12	16-4.9	4.16	0.33	0.12	30	1.5-2.9	1.97	0.30	0.11	10	3.6-5.8	4.89	0.70	0.55	
	BL	30	4.7-5.6	5.19	0.22	0.08	30	7.5-8.8	7.98	0.31	0.16	14-5.5	4.13	0.44	0.16	30	1.5-2.4	1.92	0.25	0.09	7	4.4-6.1	5.07	0.66	0.61	
	BLA	30	4.7-5.8	5.37	0.29	0.11	30	7.5-8.7	8.08	0.36	0.13	14-5.9	4.11	0.34	0.13	30	1.5-2.3	1.97	0.22	0.08	1	(5.5)				
	BRL	121	4.9-6.1	5.43	0.26	0.05	121	7.3-9.1	8.25	0.44	0.06	14-5.3	4.17	0.36	0.06	121	1.6-2.7	2.08	0.23	0.04	20	4.2-6.4	5.04	0.50	0.23	
	CL	90	4.8-6.2	5.43	0.26	0.05	90	7.3-9.3	8.18	0.40	0.07	14-5.2	4.24	0.35	0.07	90	1.7-2.7	2.11	0.21	0.05	31	4.2-6.7	5.15	0.69	0.25	
	GWA	30	5.0-5.8	5.49	0.27	0.10	30	7.5-8.7	8.18	0.35	0.16	14-5.2	4.30	0.42	0.16	30	1.7-2.6	2.09	0.22	0.08	3	4.6-6.8	5.93			
	LP	30	4.9-6.2	5.55	0.32	0.12	30	7.3-8.8	8.21	0.36	0.11	14-5.1	4.41	0.30	0.11	30	1.7-2.6	2.13	0.24	0.09	3	5.4-6.1	5.67			
	YOL	10	5.3-6.0	5.74	0.19	0.14	10	7.9-8.9	8.31	0.36	0.15	14-4.7	4.34	0.23	0.16	10	1.7-2.3	2.05	0.21	0.15	1	(5.0)				
	BP4	30	5.1-6.3	5.67	0.29	0.11	30	7.9-9.3	8.44	0.37	0.09	14-5.2	4.50	0.31	0.11	30	1.7-2.8	2.23	0.25	0.09	5	5.2-6.2	5.60	0.39	0.49	
OLP	OLP	14	5.4-6.4	5.87	0.32	0.19	14	8.0-9.4	8.58	0.40	0.20	14-4.9	4.51	0.34	0.20	14	1.8-2.7	2.24	0.24	0.14						
	OLP1	30	5.2-6.2	5.78	0.29	0.11	30	7.5-9.7	8.69	0.53	0.16	14-5.8	4.52	0.43	0.16	30	1.6-2.8	2.19	0.30	0.11	11	4.8-6.3	5.50	0.52	0.35	
	OLP2	30	5.3-6.4	5.82	0.26	0.10	30	7.8-9.2	8.60	0.40	0.15	14-5.5	4.64	0.40	0.15	30	1.8-3.1	2.36	0.33	0.12	30	4.6-7.5	5.71	0.67	0.25	
	OLP3	30	5.2-6.1	5.80	0.24	0.09	30	8.3-9.4	8.83	0.28	0.11	14-5.5	4.68	0.31	0.11	30	1.6-3.1	2.32	0.32	0.12	20	4.5-7.2	5.73	0.64	0.30	
	BOL	30	5.3-6.3	5.67	0.28	0.10	30	7.8-9.4	8.56	0.40	0.12	14-5.0	4.41	0.31	0.12	30	1.7-2.8	2.17	0.25	0.09	14	4.9-6.0	5.49	0.39	0.22	
	OCH	30	5.2-6.3	5.79	0.31	0.12	30	7.8-9.2	8.49	0.40	0.15	14-4.6	4.66	0.41	0.15	30	1.9-3.0	2.36	0.24	0.09	8	5.0-6.7	5.79	0.60	0.50	
BPB-C		16	4.8-5.4	5.21	0.18	0.10	16	7.8-8.8	8.29	0.33	0.18	14-4.6	4.06	0.34	0.18	16	1.7-2.4	2.03	0.18	0.10	16	4.1-6.8	5.12	0.65	0.35	

Measurements in mm.

95% = 95% confidence interval for the mean.

TABLE 40

Size variation in mandibles of *Cryptomys hottentotus* from Boomplaas A upper levels.

		A: Alveolar length					B: posterior border M ₂ -symphysis					C: attachment ascending ramus					D: foramen mentale-alveolar margin					E: depth of mandible				
		N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%	N	Range	\bar{X}	s	95%
Unit DGL																										
	DGL1	10	4.8-5.7	5.25	0.28	0.20	10	7.9-8.8	8.24	0.34	0.28	14-4.5	4.04	0.39	0.28	10	1.6-2.5	1.93	0.29	0.21	4	4.0-5.6	4.90			
	DGL2	20	4.5-5.9	5.22	0.30	0.14	20	7.5-9.0	8.19	0.38	0.16	14-4.8	4.23	0.34	0.16	20	1.6-2.3	1.93	0.17	0.08	10	4.0-6.0	4.79	0.79	0.56	
	BLD2	13	4.8-6.1	5.36	0.39	0.23	13	7.3-9.1	8.03	0.50	0.23	14-4.8	4.28	0.38	0.23	13	1.5-2.4	1.97	0.25	0.15	5	4.3-6.0	5.10	0.72	0.89	
	BLD2A	17	4.9-5.7	5.21	0.26	0.13	17	7.3-8.8	8.01	0.41	0.15	14-4.6	4.04	0.29	0.15	17	1.5-2.4	1.88	0.25	0.13	2	4.6-5.1	4.85			
Unit BRL																										
	BRL	12	5.0-5.8	5.34	0.23	0.15	12	7.3-8.5	8.03	0.40	0.25	14-4.9	4.10	0.39	0.25	12	1.7-2.6	2.04	0.23	0.14	1	(6.4)				
	BRL2	19	5.2-6.1	5.55	0.29	0.14	19	7.5-9.0	8.35	0.39	0.16	14-4.8	4.13	0.33	0.16	19	1.7-2.4	2.07	0.24	0.11	4	4.2-5.3	4.85			
	BRL4	30	5.0-6.0	5.45	0.26	0.10	30	7.5-9.0	8.32	0.42	0.13	14-5.0	4.15	0.35	0.13	30	1.6-2.5	2.07	0.24	0.09	8	4.3-5.6	5.03	0.41	0.34	
	BRL5	30	4.9-6.1	5.42	0.28	0.10	30	7.3-9.1	8.24	0.47	0.13	14-5.3	4.22	0.35	0.13	30	1.6-2.5	2.09	0.21	0.08	5	4.3-5.2	4.88	0.41	0.51	
	BRL6	30	4.9-5.8	5.39	0.24	0.09	30	7.4-9.0	8.23	0.46	0.15	14-5.1	4.21	0.39	0.15	30	1.7-2.7	2.12	0.23	0.09	2	5.1-5.2	5.15			
Unit CL																										
	BRL7	30	4.8-6.0	5.49	0.27	0.10	30	7.5-9.3	8.25	0.45	0.12	14-5.0	4.29	0.33	0.12	30	1.7-2.6	2.11	0.21	0.08	5	4.5-6.3	5.12	0.71	0.88	
	CL1	30	5.1-6.2	5.52	0.26	0.10	30	7.8-9.2	8.26	0.37	0.11	14-4.9	4.23	0.30	0.11	30	1.9-2.5	2.13	0.19	0.07	8	4.3-5.5	4.94	0.50	0.42	
	CL3BG	30	4.9-5.6	5.30	0.19	0.07	30	7.3-8.6	8.03	0.33	0.16	14-5.2	4.19	0.43	0.16	30	1.7-2.7	2.07	0.25	0.09	18	4.2-6.7	5.26	0.76	0.38	

Measurements in mm.

95% = 95% confidence interval for the mean.

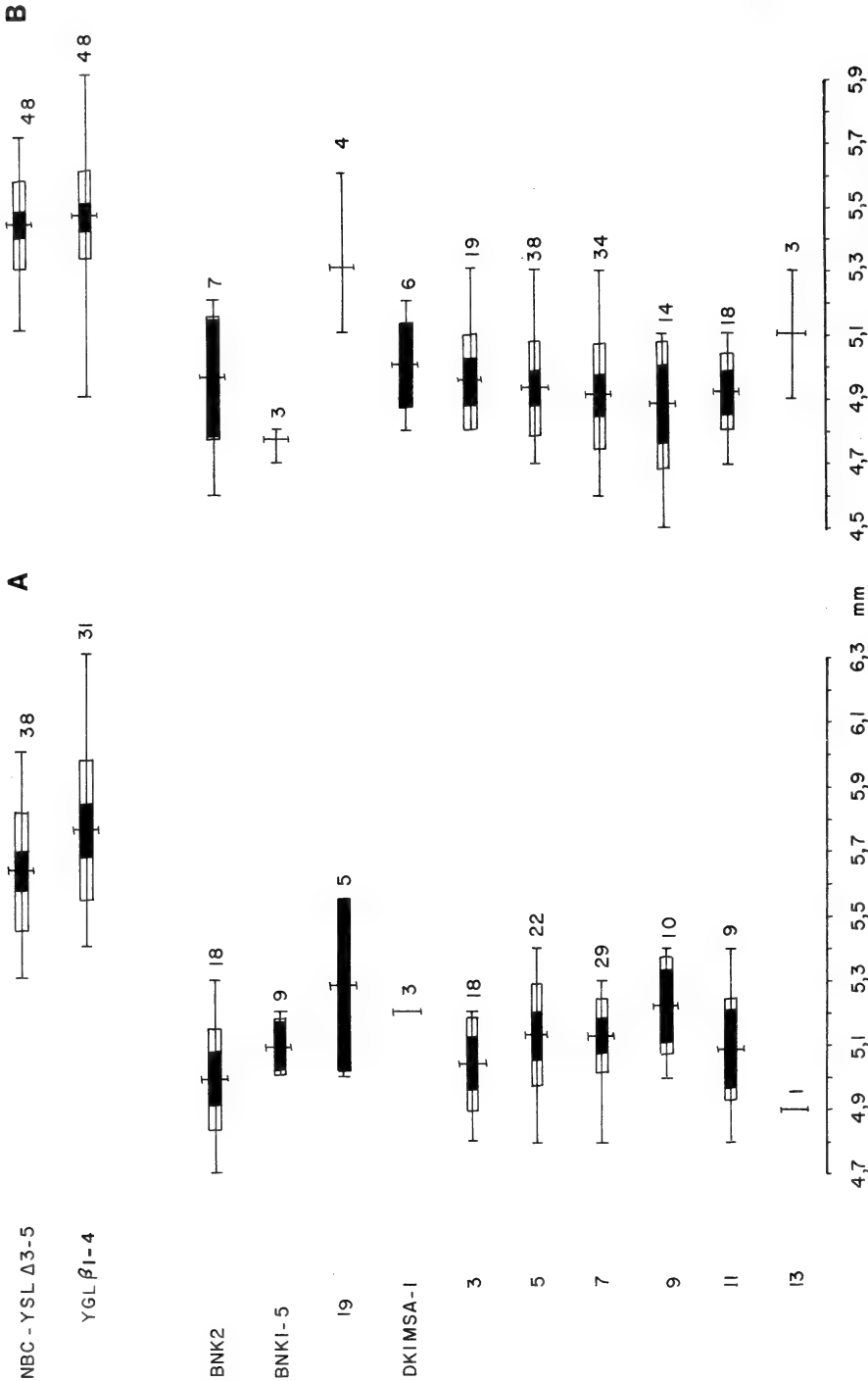


Fig. 27. Variation in parameter A, length of M_{1-2} , and parameter B, length of M_{1-2} , in *Tatera afra* from various sites.

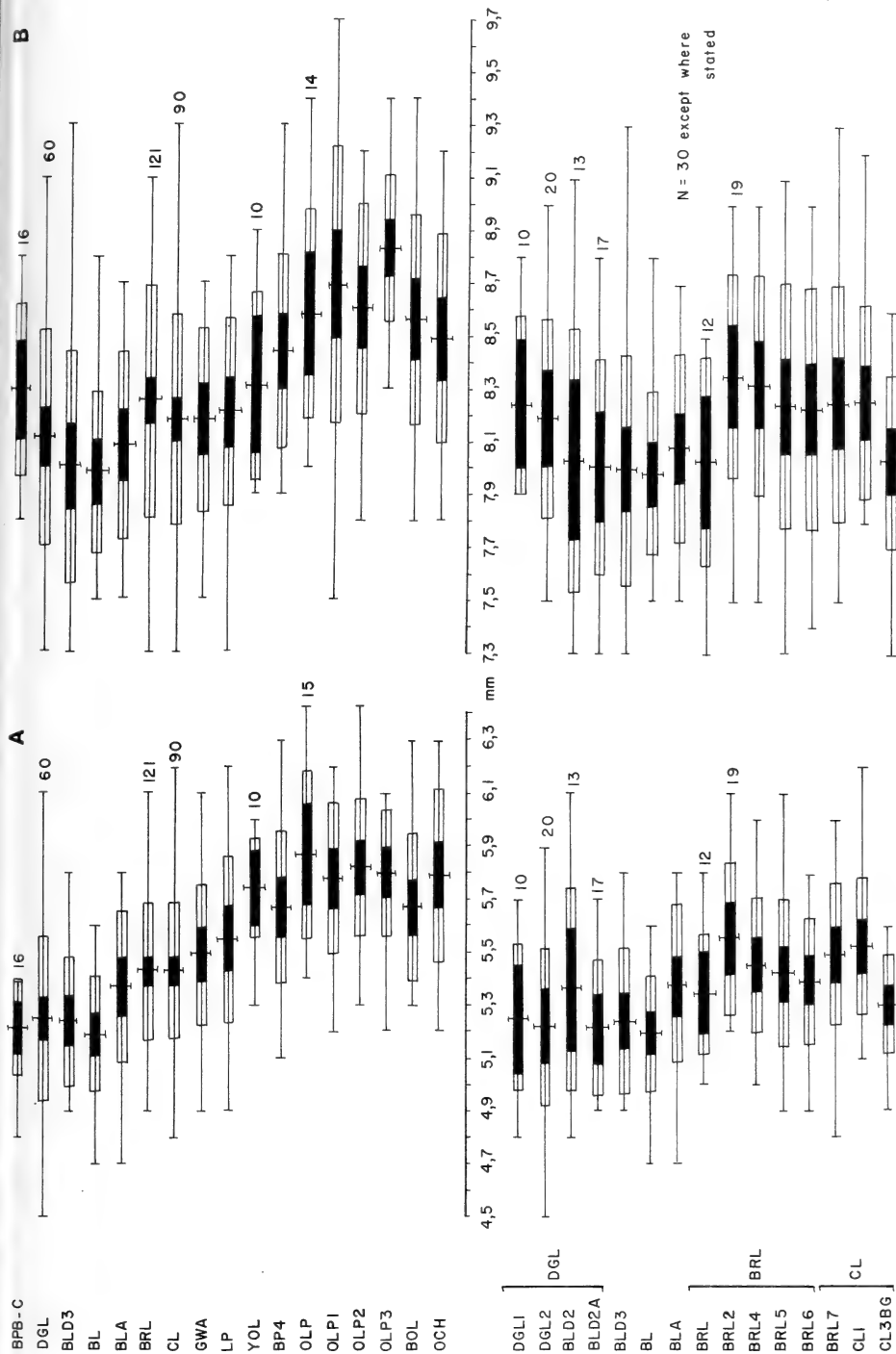


Fig. 28. Variation in parameter A, alveolar length, and parameter B, distance between the posterior borders of M_1 and symphysis, in *Cryptomys hottentotus* from Boomplaas.

variation in depth of attachment of ascending ramus and, particularly, in the two parameters related to depth of mandible.

There are very noticeable differences in the various parameters in different levels at Boomplaas A. In all the parameters except depth of mandible (Figs. 28–30) there is a tendency for a general decline in size in progressively younger samples. There appears to be some indication of a slight reverse in the trend in the uppermost levels, although this is not entirely borne out by the more detailed analysis of these levels, which will be discussed below. The depth of the mandible shows quite a different pattern, with the mean for this parameter being very much lower in the postglacial levels than in the glacial levels (Fig. 30). Such a pattern is very similar to that for *Crocidura flavescens*, which would tend to suggest a correlation with temperature. It is almost certain, however, that the pattern is the spurious result of incomplete data (Tables 39–40) and it is quite possible that, given more complete data, the pattern would be rather more like those provided by the other parameters. Under the circumstances, the main pattern is to be preferred as being based on sounder evidence.

The pattern exhibited by *C. hottentotus* is different from those found in the other species examined, except for the teeth of *Aethomys namaquensis*. As was suggested for the latter, it is unlikely that this pattern can be correlated with temperature change. If this is the case, it is possible that *C. hottentotus* is, indeed, responding to changes in rainfall, or perhaps effective precipitation. *C. hottentotus* may, as was suggested above, be showing a reaction analogous to that of *Spalax ehrenbergi* in Israel, which increases in mass with increasing rainfall (Tchernov 1968: 39). If this is so the present data would suggest a general decline in rainfall at Boomplaas during approximately the last 80 000 years. It is, however, also possible that *C. hottentotus* exhibits a reverse reaction and that decreases in mass coincide with increases in rainfall. This may, in fact, be suggested by evidence (D. M. Avery, unpublished data) that this species is smaller in the south-western Cape than it is further north. On the other hand, the fact that *C. hottentotus* is relatively small in the glacial maximum samples from Boomplaas A (Figs. 28–30), would suggest that decreases in mass and rainfall are coincident. This is because the glacial maximum is thought on other evidence to have been dry. Detailed studies will, of course, be needed to determine more precisely what correlation, if any, there is between body mass and rainfall.

The patterns exhibited by the detailed analysis of the upper levels show general consensus, except in depth of mandible which, again, is different from the others (Fig. 25). The indication is that the mean size of individual in the populations sampled in the lower half of the sequence, approximately levels CL1 to BRL2, was smaller than the mean size in the upper half. The smallest mean size apparently occurred in levels BL to BLD2A approximately. There is some partly inconsistent evidence for an increase in mean size thereafter which is most obvious in length of M_3 to symphysis. In this case the modern BPB–C sample continues the trend but in the other parameters this is not the case.

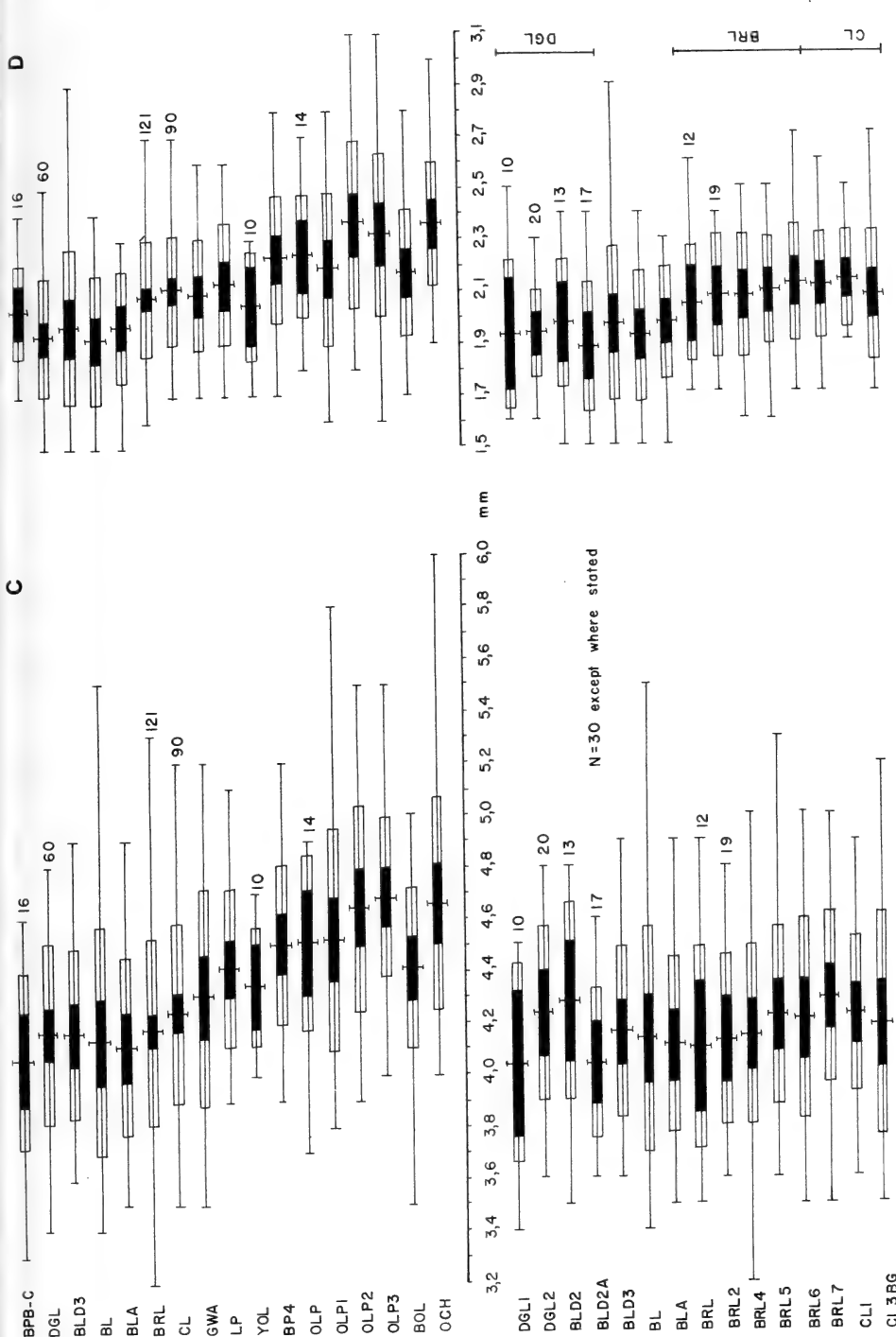


Fig. 29. Variation in parameter C, maximum depth of attachment of ascending ramus, and parameter D, distance between foramen mentale and alveolar margin, in *Cryptomys hottentotus* from Boomplaas.

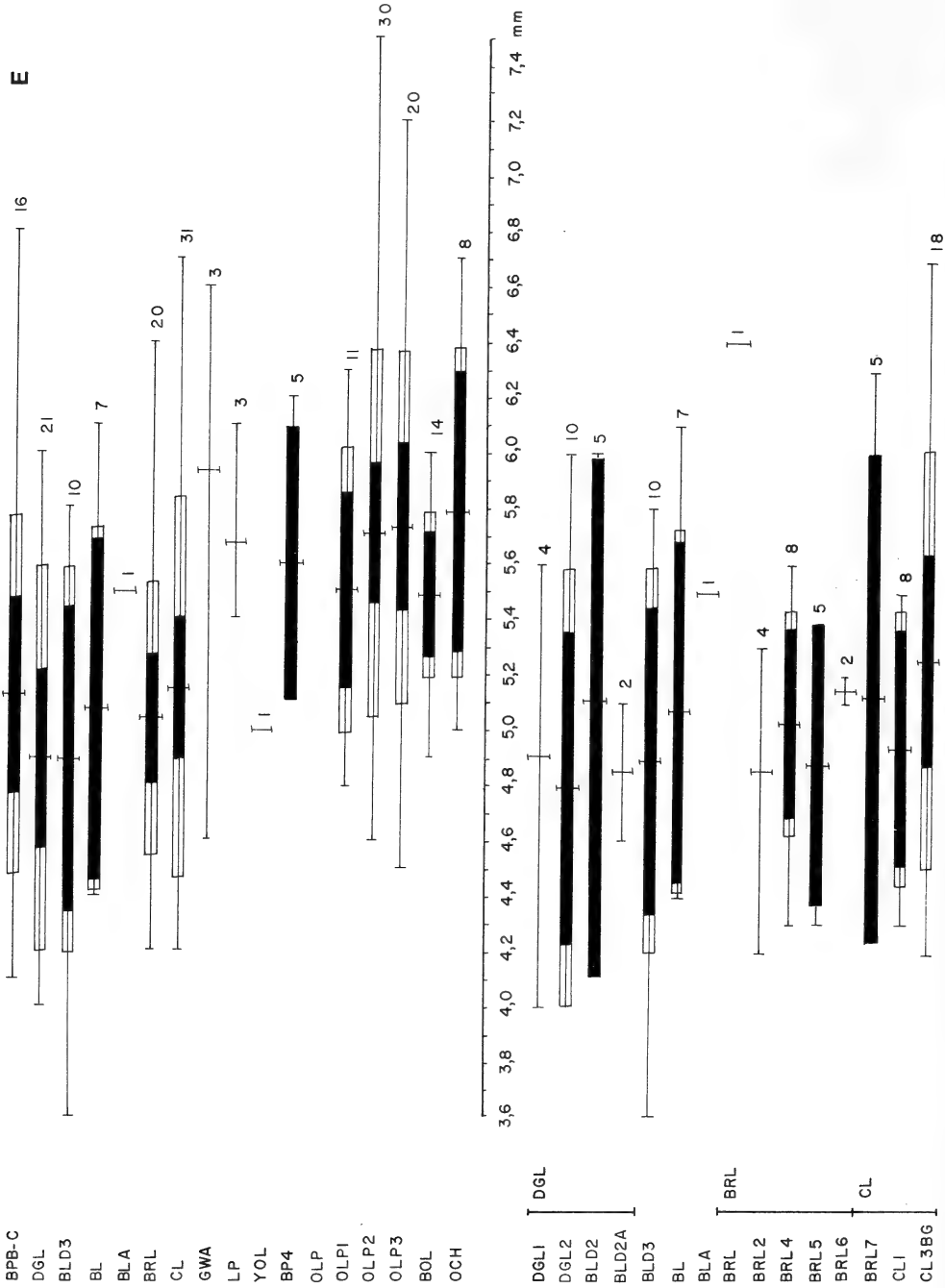


Fig. 30. Variation in parameter E, depth of mandible, in *Cryptomys hottentotus* from Boomplaas.

Although similar to the means for the material from the latest levels at BPA, the means from BPB–C tend not to conform to the trend (Fig. 25).

There is no conclusive evidence of rapid change in this species. Where 't' tests show there is significant difference in the means of successive levels (Table 41), the radiometric dating tends to indicate that a relatively long period of time is involved. Only in the case of levels OLP3 and BOL is the difference

TABLE 41
Selected 't' tests for *Cryptomys hottentotus*.

	't'	d.f.	P
A*			
BL/BLA	2,71	58	0,01
BRL/BRL2	2,12	29	0,05
OLP3/BOL	1,93	58	0,05
B			
BRL/BRL2	2,20	29	0,05–0,02
CL1/CL3BG	2,54	58	0,02–0,01
OLP2/OLP3	2,58	58	0,02–0,01
OLP3/BOL	3,03	58	0,01–0,001
C			
OLP3/BOL	3,37	58	0,001
BOL/OCH	2,66	58	0,01
D			
YOL/BP4	2,04	38	0,05
OLP1/OLP2	2,09	58	0,05
OLP3/BOL	2,02	58	0,05
BOL/OCH	3,00	58	0,01–0,001

* See Tables 39–40 for explanation of parameters and basic data.

significant in all four parameters tested. Depth of mandible was not tested because it did not appear to show any real pattern of change. The null hypothesis was two-sided in tests for this species because no assumptions could be made about the direction of size change; that is to say, it was not possible to hypothesize that the trend should be towards larger or smaller during a given period of time.

EVIDENCE FROM SPECIES DIVERSITY

It has been observed that, in general, animal life in tropical climates tends to be more abundant and varied than that in temperate climates (Krebs 1972: 500). This is, in effect, the same point as that made by Kowalski (1971: 466) and mentioned above, that mammalian communities in harsh climates contain fewer species than those in milder climates. If different climatic conditions can affect the structure of contemporary communities, it should follow that changes in community structure or species diversity in one place at different times in the past would also be due to climatic differences. Considerable differences are, in fact, noticeable in the structure of micromammalian communities of different

TABLE 42

Variation in aspects of species diversity in the Congo Valley and at Klasies River Mouth 1A, Nelson Bay Cave, and Glentyre.

	N	S	c	d	e	H
BPA: DGL	848	22	0,15	3,11	0,73	2,26
BLD3	1055	23	0,14	3,16	0,74	2,31
BL	280	21	0,12	3,55	0,80	2,44
BLA	604	23	0,16	3,44	0,73	2,27
BRL	1761	25	0,14	3,21	0,73	2,35
CL	1449	21	0,16	2,75	0,72	2,20
GWA	1805	19	0,28	2,40	0,57	1,69
LP	1839	20	0,25	2,53	0,60	1,79
LPC	140	15	0,27	2,83	0,65	1,75
YOL	315	18	0,20	2,96	0,67	1,95
BP1	353	18	0,24	2,90	0,66	1,90
BP2	110	15	0,16	2,98	0,78	2,12
BP3	93	16	0,20	3,31	0,73	2,03
BP4	1708	22	0,21	2,82	0,63	1,96
OLP	353	18	0,20	2,90	0,69	2,00
OLP1	1189	22	0,24	2,97	0,62	1,91
OLP2	9500	23	0,25	2,40	0,61	1,90
OLP3	4197	23	0,23	2,64	0,62	1,94
BOL	1802	23	0,22	2,93	0,61	1,91
BOL1-3	110	17	0,17	3,40	0,76	2,14
BOL4	106	10	0,22	1,93	0,77	1,78
BOL5	96	12	0,21	2,41	0,73	1,81
OCH	529	21	0,20	3,19	0,66	2,00
LOH	120	19	0,20	3,76	0,69	2,02
BPB	747	22	0,11	3,17	0,80	2,47
BPC	504	18	0,13	2,73	0,81	2,33
NGA	532	21	0,14	3,19	0,76	2,32
NGB	261	23	0,13	3,95	0,77	2,42
KRM1A: 6	47	10	0,14	2,34	0,92	2,12
15	103	12	0,18	2,37	0,81	2,01
16	43	8	0,24	1,86	0,81	1,69
22	42	8	0,26	1,87	0,77	1,61
32	107	10	0,36	1,93	0,64	1,47
NBC: BSL	59	8	0,35	1,72	0,68	1,42
YSL	2882	18	0,33	2,13	0,52	1,51
YGL	770	16	0,32	2,26	0,58	1,62
GLEN	542	15	0,32	2,22	0,64	1,73

N = number of individuals

S = number of species

c = dominance

d = species richness

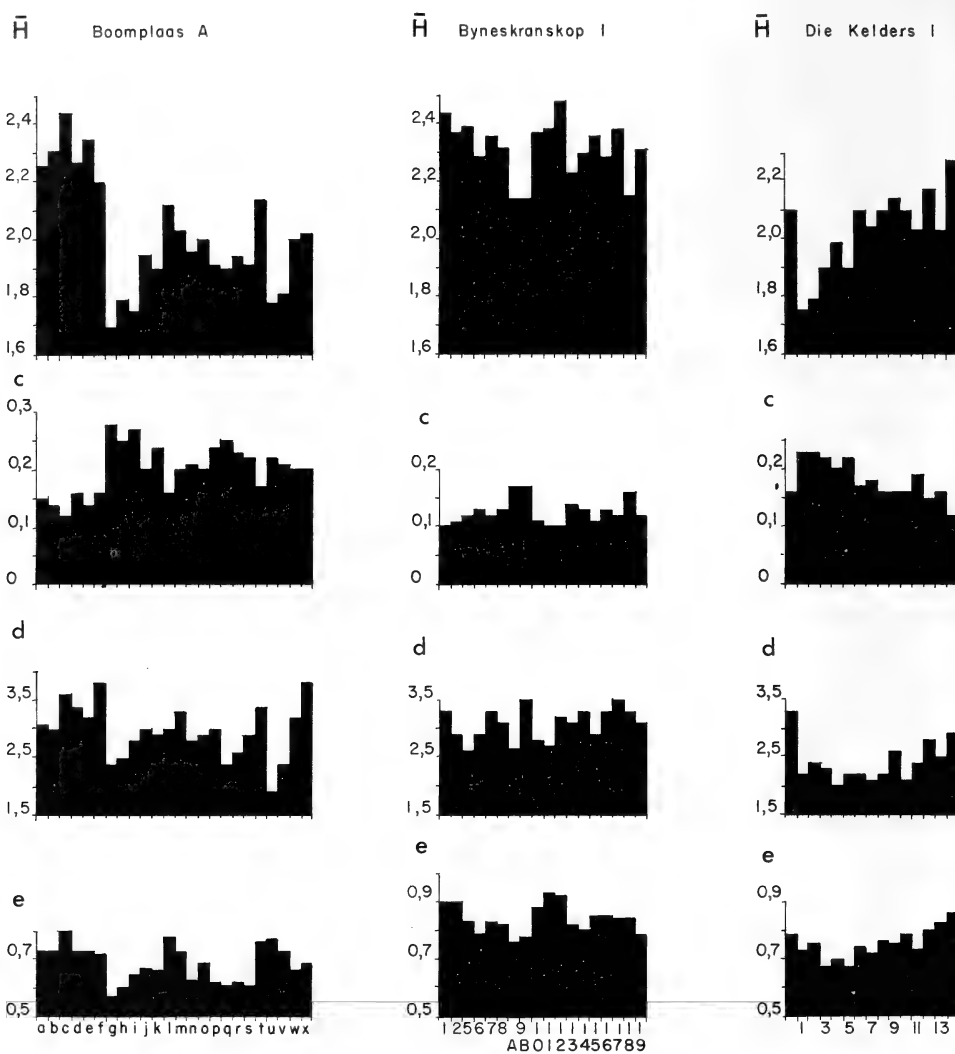
e = evenness

H = general diversity

ages both at Boomplaas A and at coastal sites. Analysis of the differences involved suggests that this line of investigation could prove useful for palaeo-environmental interpretation. In particular the general diversity index (\bar{H}) appears to conform well to known general climatic trends. Thus, \bar{H} is much higher in postglacial than in glacial communities. If glacial is taken to mean harsh conditions and postglacial, or interglacial, to mean mild conditions, this suggests that the basic hypothesis given above is true and that climatic variation is being reflected in differences in species diversity.

It is, however, important to point out here that the equation of mild conditions with interglacials, and vice versa, refers specifically to the sites discussed below and generally to any sites currently experiencing mild climates. The modern samples from the Congo valley and Byneskranskop 2 exhibit high indices and present conditions are known to be mild. Similar high indices in the Holocene may be expected to indicate conditions similar to those of the present, always assuming that the faunal list is not completely different. In areas where it can be shown that modern conditions are reflected in lower indices of diversity, interpretation would obviously have to be adapted accordingly. The index may be artificially low, as in the case of Glentyre (Table 42), the situation apparently being caused by the predator's reliance on one major prey item. In these circumstances it would be complicated to compare this sample with another. Naturally low indices would be expected in a desert or other harsh environment, so that changes in the past may conceivably include increases in diversity; in other words, the pattern may be the opposite of that observed in the southern Cape.

The index of species richness or variety (d) was calculated in order to discover whether there was any correlation between this factor and general known climatic conditions. If the situation noted by Kowalski (1971) were to find any application in the present study, the index of species richness might be expected to show this. In fact, at Boomplaas A the index is low for samples from levels LP and GWA which are known to have been accumulated during the last glacial maximum and high in the Holocene (Fig. 31). The indices for the modern samples are also high. Likewise, the indices for the Die Kelders 1 M.S.A. samples are lower than those for the L.S.A. sample and the Byneskranskop 1 samples. The BNK2 sample also has a high index. This would seem to indicate that generally this index constitutes a reliable expression of climatic conditions. It would appear, however, that minor fluctuations are more likely to be due to differences in the size of the sample than to changes in conditions. More specifically, large samples tend to have low indices of species richness, but this is almost certainly a function of the size of the sample. There would seem to be an optimum sample size which is governed by the maximum possible number of species; once all possible species are represented, any subsequent increase in the sample will merely have the effect of reducing the index of species richness. For this reason it is suspected that the indices for BPA levels OLP3 and OLP2 may have been artificially lowered. The situation



a DGL d BLA g GWA j YOL m BP3 p OLPI s BOL v BOL5
 b BLD3 e BRL h LP k BPI n BP4 q OLP2 t BOL1-3 w OCH
 c BL f CL i LPC l BP2 o OLP r OLP3 u BOL4 x LOH

Fig. 31. Aspects of community structure in samples from Boomplaas A, Byneskranskop 1 and Die Kelders 1. (\bar{H} = general diversity; c = dominance; d = species richness; e = evenness.)

at DK1 illustrates the process well. Here it would seem that the maximum possible number of species is seventeen and that an optimum sample size was approximately 1 000 since no new species were added in samples larger than that. Therefore, in levels 7 up to 3 the index of species richness is determined solely by the size of the sample. Again the index for samples from these levels will be artificially low. It would seem, therefore, that this is not an ideal index to use in the present context because of these complicating factors.

Evenness (equitability) of species representation is another aspect of diversity which required assessment. The index (e) used to express this seems to be virtually independent of sample size and, as such, is intrinsically of greater use for subfossil samples. The same general pattern emerges as for the species richness, that is, postglacial samples have a higher index than do glacial samples (Fig. 31). There are some exceptions and it is of interest to note high values for this index in samples from BPA levels BOL1 to BOL5 and again from levels BP1 and BP2. This may suggest more equable conditions during these periods. By the same token indices for samples from the lowest M.S.A. levels at DK1 fall within the range expected for interglacial conditions. Indices for BNK1 samples are generally higher than those for postglacial BPA samples, which could reflect the fact that maritime climates are normally less extreme than continental climates, especially in mountain regions. It also emphasizes the fact that comparisons can be made between different areas provided it is known that the samples are contemporary. There may thus be some potential for investigating spatial variation as well as temporal variation.

Dominance is, in effect, the converse of evenness and this is shown very clearly by the indices. Figure 31 illustrates that the index of dominance (c) varies inversely to the index of evenness. Thus, at Boomplaas A the highest index of dominance is recorded for samples from the last glacial maximum, levels LPC to GWA. Very high indices also occur for the samples from Nelson Bay Cave levels of a similar age. Holocene indices of dominance are very much lower, with a tendency to be rather lower at Byneskranskop 1 than at Boomplaas A. Indices for Die Kelders 1 are relatively low in the lower half of the M.S.A. sequence. Indeed, the index for many samples from these levels is similar to or even lower than that for the sample from Die Kelders 1 L.S.A. level 12. It would appear that either this index or the index of evenness can be used with advantage for palaeoenvironmental interpretation, but that the pattern exhibited by dominance is rather clearer.

The Shannon index of general diversity (\bar{H}), which takes into consideration both species richness and evenness, is probably the most suitable for present purposes. It is relatively unaffected by sample size, as was mentioned above, it takes the two main aspects of diversity into account and it produces a clearer pattern than any of the other indices (Fig. 31). At Boomplaas A there is a striking difference between the high indices for the postglacial samples and the low indices for the glacial samples with no overlap between the two (Fig. 31, Table 42). Even in the case of Byneskranskop 1 and the Die Kelders 1 M.S.A.

samples, where the distinction tended to be less clear in the individual indices, there is little overlap. The dividing-line between what may be termed the glacial and interglacial values of the index would appear to fall somewhere between 2,10 and 2,20. It is also noticeable that coastal and inland samples seem to be directly comparable, with very similar values.

At Boomplaas A the lowest diversity occurs in samples from levels BOL4 and BOL5 and again in levels LPC to GWA (Fig. 31). Since the latter are known to have been deposited during the last glacial maximum, it would appear that the earlier samples were accumulated during the previous glacial maximum. The period between the two maxima seems to have been rather more moderate, with peaks of improvement in levels BOL1 and BP2. After BP2 there is a general reduction in diversity until level GWA. Thereafter, a major amelioration is indicated which is maintained, with minor fluctuations, throughout the Holocene.

In the Die Kelders 1 M.S.A. samples, diversity shows a general reduction in progressively younger samples (Fig. 31). This is particularly noticeable in the five upper levels where the youngest sample has the lowest index. This suggests that the onset of glacial maximum conditions in the area occurred at this time. The lowest level, on the other hand, has a much higher index than the others, well within the range for Byneskranskop 1 samples, which indicates a mild climate when the site was first occupied. Indices for samples from levels 13 to 6 fluctuate but tend to be relatively high, suggestive of intermediate conditions. The L.S.A. level has a low index for a Holocene sample. Whether this is due to climatic conditions or to a biased sample is not known, but is perhaps likely to be the latter. This is partly because the sample was derived from a shell midden where conditions are unlikely to have been ideal for the preservation of small mammal bones but mainly because the index for the youngest sample at Byneskranskop 1 is high. Being part of a sequence it seems reliable and suggests that the Die Kelders 1 index is too low.

The indices for samples from Byneskranskop 1 indicate that there were two periods of harsher climate, one in level 18 and a second in levels 9A and 9B. The former may have been about 10 000 B.P. and the latter is about 6 200 B.P. Between these two there was apparently a peak in level 12 perhaps about 8 000 B.P. The upper levels indicate a general improvement in the climate after about 6 200 B.P. until the top of the sequence about 1 850 B.P. Byneskranskop 2 has a much higher index than any of the subfossil samples which is difficult to explain but may be due to the much higher number of species present (Table 43).

Nelson Bay Cave samples have low indices as might be expected for glacial samples. The indices for Klasies River Mouth 1A rise from the oldest to the youngest but are still low throughout. It is, however, almost certain that the results for this site are affected by the fact that not all the microfauna was collected. If, as was apparently the case, only larger species were collected this would tend to reduce species richness and could introduce artificially high

TABLE 43

Variation in aspects of species diversity at Byneskranskop and Die Kelders 1.

	N	S	c	d	e	\bar{H}
BNK1: 1a	40	12	0,11	2,98	0,94	2,34
1b	40	13	0,11	3,25	0,91	2,34
1(a+b)	71	15	0,10	3,28	0,90	2,44
2	22	10	0,13	2,91	0,94	2,17
3	5	4	0,28	1,86	0,96	1,33
4	57	14	0,11	3,22	0,90	2,38
2-4	84	14	0,11	2,93	0,90	2,37
5	771	18	0,12	2,56	0,83	2,39
6	361	18	0,13	2,89	0,79	2,29
7	130	17	0,12	3,29	0,83	2,36
8	179	17	0,13	3,08	0,82	2,32
9A	414	17	0,17	2,66	0,76	2,14
9B	77	16	0,17	3,45	0,77	2,14
10	151	15	0,11	2,79	0,88	2,37
11	81	13	0,10	2,73	0,93	2,39
12	75	15	0,10	3,24	0,92	2,48
13	88	15	0,14	3,13	0,82	2,23
14	169	18	0,13	3,31	0,80	2,30
15	172	16	0,11	2,91	0,85	2,36
16	70	15	0,13	3,30	0,85	2,29
17	104	17	0,12	3,45	0,84	2,38
18	37	13	0,16	3,32	0,84	2,15
19	361	19	0,12	3,06	0,78	2,31
BNK2	753	23	0,09	3,32	0,84	2,64
DK1: LSA 12	74	15	0,16	3,25	0,78	2,10
MSA 1	87	11	0,23	2,24	0,73	1,75
2	64	11	0,23	2,40	0,75	1,79
3	1115	17	0,22	2,28	0,67	1,90
4	3474	17	0,20	1,96	0,70	1,99
5	1538	17	0,22	2,18	0,67	1,90
6	1538	17	0,17	2,18	0,74	2,10
7	2234	17	0,18	2,07	0,72	2,04
8	903	16	0,16	2,20	0,76	2,10
9	473	17	0,16	2,60	0,75	2,14
10	826	15	0,16	2,08	0,78	2,10
11	522	16	0,19	2,40	0,73	2,03
12	151	15	0,15	2,79	0,80	2,17
13	87	12	0,16	2,46	0,82	2,03
14	94	14	0,12	2,86	0,86	2,27

N = numbers of individuals

S = numbers of species

c = dominance

d = species richness

e = evenness

 \bar{H} = general diversity

dominance of certain species. It is possible that the general trend is accurately reflected if the same biases are present in all samples, although it is interesting that this trend is the opposite of what might be expected on other evidence. On balance, because of the unknown extent of the bias, it was considered that results for this site should probably be discounted until more reliable samples can be obtained.

PALAEOENVIRONMENTAL RECONSTRUCTION BASED ON MICRO-MAMMALIAN EVIDENCE

Reconstruction of past environments on the basis of the micromammalian evidence takes into account all the data from the different lines of investigation. Generally these are not at variance with each other, but where they are an explanation must be sought which could account for the apparent anomaly. In the present exercise it would appear logical to work from the particular to the general. For this reason the data for the three main individual sites are examined first. All the evidence for the coastal area is then considered as a unit. Finally, the complete coastal sequence is compared with that from the Congo valley in order to assess the degree of difference or similarity between the sequences of the two areas, and to make some general interpretation for the whole region if possible.

BOOMPLAAS A

Variation in all aspects of the small-mammal community examined indicates extensive change in the environment of the site during the period of its occupation. In general the various lines of evidence are in agreement. The basic pattern, with vegetational interpretation, is provided by the factor analysis of community composition. Variation in mean size of selected species has been taken as indicating changes in climate which can also be referred to the basic framework. Variation in species diversity or community structure has been used to provide general confirmation of the relative harshness or mildness of conditions, effectively climate, at various times during the period under discussion.

The BPA sequence has been divided into five palaeoenvironmental units (Table 44) on the basis of the factor analysis (Table 16). Of these the oldest, unit 5, refers to the period represented by levels LOH up to BOL1. This unit is, in fact, not homogeneous and should perhaps be considered in terms of three sub-units. Samples from levels LOH and OCH probably represent the early glacial period, as was mentioned above. The factor analysis suggests that this was a period of intermediate conditions with a slight indication of deterioration towards glacial conditions. The general indication from *Crocidura flavescens* and from the general diversity index is also of moderate conditions, that is, those approximately intermediate between full glacial and interglacial. *Myosorex varius* suggests that conditions may even have been nearer those

TABLE 44

Sequence of levels at Boomplaas A with radiocarbon dates, cultural units and palaeo-environmental interpretation.

Dates B.P.	Culture	Levels	Vegetation	Climate	General
Holocene 1 630 ± 50	Herder	DGL	Unit 1 scrub on hillsides, sparse ?semi-arid in places, elsewhere ?dense microphyllous; fairly open grass, ?trees on valley floor, extensive dense riverside reeds or grass	fluctuating	mildest in BL
1 955 ± 65		BLD3		rapid temperature rise	
6 400 ± 75	Wilton	BL			
9 100 ± 135		BLA			
10 425 ± 125	Albany	BRL		fluctuating rapid temperature rise	
Upper Pleistocene 12 425 ± 130					
14 200 ± 240	Robberg	CL	UNIT 2 transitional between Unit 1 and Unit 3	becoming warmer	mild
		GWA			
	Undefined LSA industry	LP	UNIT 3 generally fairly open, ?semi-arid on valley floor; reduced dense reeds or grass along river; restioid or 'grassy' vege- tation on hillsides; BP1 conditions rather more moderate than general	coldest	harsh
21 100 ± 420		LPC			
		YOL			moderate
		BP1			
		BP2			
		BP3			mild
32 400 ± 420					
		BP4	UNIT 4 fairly extensive dense vegetation on valley floor; extensive restioid or 'grassy' element on hillsides plus some ?semi-arid vegetation (conditions harsher than general in OLP)		
		OLP			
		OLP1			
		OLP2			
		OLP3			
		BOL		relatively warm	
		BOL1	UNIT 5 general increase in scrub on hillsides, grass on valley floor and dense riverside vegetation: BOL5 glacial maximum as in Unit 3		mild
		BOL4			harsh
		BOL5			
		OCH	period of change, ?becoming drier, more open vegetation		
		LOH		warm	moderate

pertaining in the Holocene. This is not entirely inconsistent with the evidence from *Crocidura flavescens* and it could perhaps be the case. There remains, however, the possibility that *Myosorex varius* is responding to more than one climatic factor.

The sample from level BOL5 indicates full glacial conditions, on the evidence of the factor analysis, with the samples from levels BOL4 and BOL1 suggesting progressive amelioration thereafter. At the time of level BOL5 the vegetation was probably fairly open but with a moderate amount of dense grass or reeds along the river. Elsewhere grass and some semi-arid scrub are indicated on the valley floor and a restioid or 'grassy' element apparently

dominated the hillsides. (It should be noted that here and elsewhere the term restioid or 'grassy' is employed to indicate a broad vegetation category; the specific type of vegetation will clearly vary from one place to another but cannot necessarily be identified from the small-mammal data.) An increase in the Holocene element in level BOL4 and, particularly, in level BOL1 would suggest rather more scrub on the hillsides, a reduction in semi-arid scrub and an increase in denser vegetation generally. The diversity indices confirm the suggestion that at the time of level BOL5 the climate was harsh. They also indicate that conditions were as harsh during the time that level BOL4 was accumulated but that they were considerably milder during the time of level BOL1. The general indication is that although levels BOL5 and BOL4 were deposited during a glacial maximum, this was rather less severe than the subsequent one which is discussed below.

Palaeoenvironmental unit 4 refers to the period represented by samples from levels BOL up to BP4. These levels appear to have been deposited during an interstadial in the Last Glacial when conditions were approximately intermediate between full glacial and interglacial. On the valley floor there would appear to have been fairly extensive dense vegetation but on the hillsides the open restioid or 'grassy' element would seem to have predominated with, possibly, a smaller semi-arid scrub element on the lower hillslopes. It is possible that the restioid or 'grassy' element is that which is today called Dense Restioid-Proteoid Shrubland (Moffett & Deacon 1977) and confined to higher altitudes, especially where conditions are relatively dry. At the time of level OLP conditions may have deteriorated somewhat. The evidence from *Crociodura flavescens* indicates that the period of level BOL was relatively warm. There is an apparent inconsistency in the temperature data. The *C. flavescens* data suggest that the period covered by levels OLP and BP4 may have been warmer than that represented by levels BOL to OLP1; *Myosorex varius* suggests the opposite. The diversity indices suggest that the samples from all these levels were accumulated under moderate conditions and it is probably preferable to accept this generalization until it becomes possible to clarify the situation.

Palaeoenvironmental unit 3 refers to conditions pertaining during the period represented by levels BP3 up to GWA. Radiometric dating indicates that this period lasted from approximately 30 000 B.P. to about 15 000 B.P. As has been pointed out previously, this is known to include the last glacial maximum and there is no difficulty in interpreting the micromammalian evidence in the light of this fact. The factor analysis suggests that conditions at the time of level BP1 were rather milder than general for this period. The overall pattern indicates fairly open vegetation with a reduced amount of dense grass or reeds along the riverside. Grass and probably semi-arid scrub occurred elsewhere on the valley floor. Indeed, the relatively high proportions of *Otomys unisulcatus* during this period suggest that semi-arid scrub was at its maximum extent and that the climate must have been drier than at any other time.

Moreover, A. Scholtz (1979 pers. comm.) has pollen evidence to suggest dry hillside scrub during this period. The micromammalian evidence suggests that the predominant vegetation type on the hillsides was restioid or 'grassy' and open. The absence of *Crocidura cyanea* from the fauna during this period is thought to be indicative of a cold climate, whether in the form of generally depressed temperatures or of very cold winters. At the same time the presence of semi-arid scrub in the valley would suggest dry conditions. Mean size of *Crocidura flavescens* indicates that the climate was coldest during the time that levels YOL to GWA were deposited, perhaps from 25 000 B.P. to 15 000 B.P., and the diversity indices confirm this suggestion. These indices further suggest that conditions were mild when levels BP3 and BP2 were deposited and moderate during the deposition of levels BP1 and YOL. The situation regarding level BP1 has already been discussed and the factor analysis, particularly the Oblique solution, may be interpreted as supporting the suggestion concerning levels BP3 and BP2. For level YOL, however, the evidence is conflicting. The factor analysis and *C. flavescens* indicate that, far from being moderate, conditions may have been at their most extreme during this period. It is difficult to explain this, although it is possible that the difference between moderate and extreme may not be as great as might appear to be the case. It is also possible that an increase in the *C. flavescens* sample may help to clarify the situation.

Following the last glacial maximum, a transitional period represented by samples from the CL levels forms palaeoenvironmental unit 2. The period involved is approximately 15 000 B.P. to 11 000 B.P. Unit CL appears to represent a combination of Holocene and interstadial elements, according to the factor analysis, while the individual levels show a clear trend from the glacial to the Holocene in each succeeding level. A large increase in dense vegetation, together with a decrease in the restioid or 'grassy' element on the hillsides, is indicated. There was also an increase in sparse, possibly semi-arid, scrub on the hillsides, but a disappearance of this vegetation type on the valley floor. As may be expected a general increase in temperature is indicated. The diversity indices show the climate to have been mild and much closer to that of the Holocene than to that of the remainder of the Upper Pleistocene.

Palaeoenvironmental unit 1 refers to the Holocene postglacial period represented by levels BRL up to DGL. The samples from these levels are consistently shown by the factor analysis to indicate a quite different set of conditions from those indicated by the samples from the Upper Pleistocene glacial levels. In general there appears to have been scrub on the hillsides, sparse and possibly semi-arid in places but elsewhere perhaps dense and microphyllous. On the valley floor fairly open grass with possibly some trees probably grew. Relatively extensive dense riverside grass or reeds are also suggested and it is possible that the trees were, in fact, mostly confined to the area along the edges of the river. While the main trend was apparently towards higher temperatures there is evidence of two periods of fluctuation; one is in unit BRL, between about 10 500 B.P. and 9 000 B.P., and the other is in unit

DGL, about 1 600 B.P. (Fig. 15). There is also an indication of two periods of accelerated increase in temperature; one of these is between levels BRL6 and BRL5, about 10 000 B.P., and the other is between levels BLD3 and BLD2A, about 2 000 B.P. During the time of unit BRL, the climate apparently continued to be moderately dry, as is suggested by the relatively high proportion of sparse possibly semi-arid scrub on the hillsides and even a relative increase in semi-arid scrub on the valley floor.

It should be noted at this stage that there may be a restriction on interpretation. This is related to the inequality of the time periods represented by the different units in the archaeological sequence. At Boomplaas A, for instance, some levels such as YOL may represent up to 10 000 years, whereas others such as BP2 may represent only a few hundred years (H. J. Deacon 1979 pers. comm.). This could have a bearing on the amplitude of the trends being reflected in the micromammalian evidence. The results of the factor analysis suggest, in fact, that there exists an overall pattern of long-term trends. Within these trends the evidence from individual species may indicate lesser fluctuations where shorter time periods can be recognized. It would seem, therefore, that where there is a long sequence it should generally be possible to identify major trends, but only where that sequence is divided into short-term units will it be possible to identify lesser fluctuations.

BYNESKRANSKOP 1

The series of micromammalian samples from Byneskranskop 1 provides evidence for the last 13 000 years (Table 45). This includes the late glacial period at the end of the Upper Pleistocene and the postglacial period or Present Interglacial in the Holocene. The series has been divided into three palaeoenvironmental units on the basis of the factor analysis. Climatic data for individual species are sparse but species diversity provides some indication of changing conditions.

Palaeoenvironmental unit 3 encompasses the earlier half of the period, from about 13 000 B.P. to 6 500 B.P., and involves the samples from levels 19 up to 11 inclusive. The indication is that extensive, possibly fairly closed, grass occupied the flats. Pans, which may suggest a relatively or seasonally wet climate, are also indicated on the flats, as is a certain amount of scrub. Considerable dense vegetation apparently existed along the river banks and on the lower hillsides; it is possible, in fact, that the entire area between the Uilenkraal River and Byneskranskop was so covered. On the hills themselves there was a prominent restioid or 'grassy' element, especially at the time when level 13 was deposited. There may also have been a proteoid element on some of the hills as there is today (Schweitzer & Wilson 1978). The diversity indices suggest that conditions were relatively harsh at the time that level 18 was deposited and less mild than usual at the time of level 13. This latter agrees with the suggestion, made above, that the restioid or 'grassy' element was most prominent at this time, using the analogy indicated for Boomplaas A. The

TABLE 45

Sequence of levels at Byneskranskop 1 with radiocarbon dates, cultural units and palaeo-environmental interpretation.

Dates B.P.	Culture	Levels	Vegetation	Climate	General
1 880 ± 50	E	1	UNIT 1 intermediate as unit 3 but more scrub and less restioid vegetation on hills	warmer	1 mildest
3 220 ± 45		2-4			mild
3 400 ± 55					
3 900 ± 55	Wilton D	5	UNIT 2 extensive ?more open grass on flats; rather less restioid or 'grassy' vegetation on hills and more scrub; less dense vegetation near river and lower slopes (?relatively dry)		
		6			
		7			moderate
		8			
6 370 ± 90	D	9A			
6 100 ± 140		9B			harsh
6 540 ± 55		10	changing vegetation		
	C	11	UNIT 3		mild
		12	extensive dense vegetation near river and lower hillslopes; extensive ?more closed grass on flats with pans and some low scrub; restioid or 'grassy' ?and proteoid element on hillsides (peak restioid element in level 13)		12 mildest
		13			
9 760 ± 85	Pre-Wilton	14		general increase in temperature	13 rather harsher
		15	(?relatively wet)		moderate
	B	16		cooler	
		17			
		18			18 harsh
12 730 ± 185	A	19			19 moderate

period represented by levels 12 and 11, perhaps from 8 000 B.P. to 6 500 B.P., apparently enjoyed a milder than general climate, especially during the earlier part. In this context it should be pointed out that in this section references to mild or harsh conditions are to be understood as being within the general Holocene range; the amplitude is not comparable to that found at Boomplaas A (see Fig. 31 and Tables 42-43).

In palaeoenvironmental unit 2, the period from about 6 500 B.P. to approximately 3 500 B.P. is covered by samples from levels 10 up to 5 inclusive. The factor analysis shows that the time when levels 11 and 10 were being deposited was a period when the vegetation was changing from that of unit 3 to that of unit 2. In unit 2 there appears still to have been extensive grass on the flats but it is possible that it had become more open and that ground conditions were drier. The apparent reduction in the number of pans would suggest the same. There seems to have been a reduction in the amount of dense vegetation on the river banks and on the lower hillsides. Grass would perhaps have migrated into the area between the river and Byneskranskop. On the hillsides there is an indication that to a certain extent scrub increased at the expense of the restioid or 'grassy' element. Diversity indices suggest that, after an initially mild period from about 6 500 B.P. to 6 100 B.P., there was a short period perhaps about 6 000 B.P. when conditions were relatively harsh. There-

after, in the last part, perhaps from 3 900 B.P. to 3 500 B.P., after a period of moderate conditions, they again became mild. The evidence from *Crocidura flavescens* indicates that at this time temperatures were considerably higher than they were at about 12 700 B.P. This suggests a general warming trend, as might have been expected, but it would have been interesting to know whether there were fluctuations in the period between the two extremes.

Palaeoenvironmental unit 1 covers the latest period, from about 3 500 B.P. to 1 800 B.P., represented by samples from the top four levels. The factor analysis indicates that the sample from combined level 2–4 is very similar to those comprising unit 3. The level 2–4 sample suggests, however, that while the vegetation was generally similar, there was probably more scrub and less restioid or ‘grassy’ vegetation on the hills in the later period (about 3 500 B.P. to 3 200 B.P.). The diversity index suggests that conditions were milder than during the earlier period, which agrees with the vegetational evidence. The evidence from the sample from level 1 suggests intermediate conditions, apparently indicative of a return to more open vegetation. The evidence could, of course, be influenced by the fact that a long period of time is involved. It is of interest to note, however, that the general diversity index is the same for the upper and lower parts of level 1 (Table 43). This suggests that conditions cannot have been greatly different at 1 800 B.P. from those pertaining at 3 200 B.P. although there could still have been changes at some time between these two dates. In general, however, the indication is that conditions during this later period were milder than at any time since those indicated by the sample from level 12.

DIE KELDERS 1 MIDDLE STONE AGE SAMPLES

The series of samples from the M.S.A. levels at Die Kelders 1 provides evidence of conditions during a period of possibly some 40 000 years during the Upper Pleistocene. The sequence has been divided into three palaeoenvironmental units on the basis of the results of the factor analysis (Table 19). There are few climatic data available from individual species but the evidence from species diversity or community structure provides a general indication of prevailing conditions. Because Die Kelders 1 is situated on the present coast, there is also the possibility that the data provide some indication of sea-level changes, although this is tenuous.

The samples from the lowest three levels, 14 up to 12, comprise palaeoenvironmental unit 3 (Table 46). The evidence suggests that during this period there was extensive grassland on the flat ground which may also have existed below the cave as well as above it. Extensive dense vegetation may perhaps have been situated near a marsh or lake which is currently submerged. Both these lines of evidence may suggest that the sea-level was relatively low during this period. On the hillsides the dominant vegetation was apparently of an open restioid or ‘grassy’ type. The general indication is that conditions were relatively cold and rather wet. In level 12 there is some slight evidence for changing conditions.

Palaeoenvironmental unit 2 comprises the samples from levels 11 up to 3, although the sample from the latter level shows that conditions were intermediate at that time (Table 46). In general there is evidence for reduced grass and dense vegetation on the flats. Because there is no evidence for a compensatory increase in another type of vegetation, it is suggested that the sea-level was higher during this period and that there was actually less level ground available. It may also be that an expansion of neighbouring sand-dunes reduced the available habitat. The dominant hillside vegetation remained restioid or 'grassy' but the proportion was reduced, again without compensatory increase in another type of vegetation. The tendency for small species to predominate suggests a generally fairly open vegetation. There is also some indication that the climate was rather warmer and drier than it was during the previous period.

The samples from levels 1 and 2 comprise palaeoenvironmental unit 1 (Table 46). The indication is that conditions during this period were very similar to those pertaining during the earliest period. Thus there was again an increase in grass and dense vegetation on the flats with the possibility of a renewed lowering of the sea-level. On the hillsides, however, scrub appears to

TABLE 46

Sequence of Middle Stone Age levels at Die Kelders 1 with palaeoenvironmental interpretation and approximate dates (after Tankard & Schweitzer 1974).

Approx. dates B.P.	Level	Vegetation	Climate	General	Sea-level	
35 000	1	UNIT 1 extensive grass, dense vegetation on flats; scrub on hills	? general increase in temperature	?? wet	? lower	
	2					
	3	UNIT 2 3 intermediate		?? dry		? higher
	4					
	5	reduced grass, dense vegetation on flats; moderate restioid or 'grassy' vegetation on hills		generally mild conditions perhaps deteriorating gradually		
	6					
	7					
	8					
	9					
	10					
	11					
80 000	12	UNIT 3 12 slight change; extensive grass, dense vegetation on flats; restioid or 'grassy' vegetation on hills				? lower
	13					
	14					

have replaced the restioid or 'grassy' element and the general indication is that the climate may have been rather warmer and wetter than it was during the preceding period.

As was mentioned above, data from individual species are few so that any interpretation is necessarily uncertain. However, the evidence from *Myosorex varius* (Table 36) suggests that there might have been an increase in temperature at the time of level 8 compared with that pertaining when levels 4 and 11 were deposited. The evidence from *Crocidura flavescens* (Tables 30–32) indicates a general increase in temperature from the time that level 10 was deposited to that of level 6 and then level 4. These data may be less reliable because they are based on fewer observations. Both sets of data suggest temperatures might have been higher even than they were during the Holocene and thus confirm the suggestion that conditions were mild during this period. As has been pointed out above, the data for *Tatera afra* are not yet adequate for palaeoenvironmental interpretation. Information for this species has not, therefore, been considered here.

The information available from species diversity does not appear to agree entirely with the evidence from other lines of investigation. There is a general decline in the index of general diversity from the beginning of the period to the end (Fig. 31, Table 43). This would suggest a trend towards harsher conditions which are not otherwise apparently indicated. In fact, this is relative and for the earlier samples, from levels 14 up to 5, the index is within the range exhibited by Holocene samples from Byneskranskop 1. This would then confirm that conditions were comparatively mild during that period. The low index for the later samples is largely due to an increase in dominance rather than to other factors (Fig. 31, Table 43). There are two reasons for suggesting that this increase in dominance may be due to factors other than climatic conditions. In the first place, the two dominant species are not the same in all five samples. This would suggest that the vegetation—and presumably therefore the climate—must, in fact, have changed during this period. Secondly, *Otomys irroratus*, which is one of the dominants in the samples from the upper levels, is normally associated with mild conditions. On the other hand, it could perhaps be that extremes in available moisture are being monitored. This might indicate dry conditions during the time that levels 5 up to 3 were deposited and wet conditions during the time when levels 2 and 1 were deposited. It is, however, perhaps unlikely that conditions could have been sufficiently extreme to affect the diversity in this way, especially since the same three species are most numerous throughout the sequence, but in differing proportions.

COASTAL SAMPLES

Conditions pertaining at Die Kelders 1 during the time when the M.S.A. levels were being deposited are shown to have been different from those at Byneskranskop 1. This could be expected in view of the fact that the latter is a Holocene site and the former is thought to be an Upper Pleistocene site. It is

necessary, however, to attempt to establish how much of the difference is due to climate and vegetation and how much to topography. It is clear, for instance, that the species that occur in higher quantities at BNK1 are plains and lower hillside animals. The inference is that these niches were reduced in the DK1 area. In fact, it has been suggested above that the area of flat ground below the cave at DK1 fluctuated but was perhaps unlikely to have been extensive at any time when the site was occupied. It is also possible that the nature of the cliffs is not such as to provide a suitable habitat for some of the species which occurred at BNK1.

Variation within the site may, however, provide some insight into the relative situation. At DK1 in the majority of the levels *Myosorex varius* is present in much higher proportions than *Otomys irroratus*, which suggests a relatively dry climate. At BNK1 the situation tends to be similar in the upper half of the sequence but not in the lower half. In general, therefore, it would appear that the Holocene was rather wetter than the Upper Pleistocene on the coast. This accords with the interpretation of the sequence at Boomplaas A. At both sites it would appear that the restioid or 'grassy' vegetation generally predominated on the hillsides. The only exceptions to this were in the latest part of the DK1 M.S.A. sequence and in the DK1 L.S.A. level 12 and BNK2 samples. The evidence from *Crocidura flavescens* and *Myosorex varius* is not really adequate for sound interpretation. It appears to be conflicting, at least in part, but this may be due to the fact that complete sequences are not available. As was mentioned above, the general diversity for the lower half of the DK1 M.S.A. sequence falls within the range for the BNK1 sequence. This would suggest that conditions were not dissimilar during these periods at the two sites.

The modern (BNK2) and late Holocene (DK1 L.S.A. level 12) samples suggest that conditions were different in this period from either of the two earlier periods. The DK1 L.S.A. sample indicates that possibly conditions were similar to those pertaining during the central part of the M.S.A. period but that there was replacement of grass by scrub on the hillsides. *Steatomys krebsi* replaced *Tatera afra* as the dominant plains animal as it did in apparently drier times at Byneskranskop 1. Dense waterside vegetation was apparently an important vegetational feature as it had been during the M.S.A. It was, however, presumably located on the present coastal plain since the sea-level would have risen to its present level before about 2 000 B.P. when the site was reoccupied. Perhaps rather wetter conditions are suggested by the BNK2 sample, with relatively extensive dense waterside vegetation. The replacement of grass by scrub on the hillsides is confirmed.

HOLOCENE AND MODERN SAMPLES

The factor analysis shows that there is a basic difference between the Boomplaas A, Byneskranskop 1 and modern samples. In the case of the two Holocene samples this is possibly due to differences in topography, as was suggested in the previous analysis. Certainly variation in the proportions of the

individual species shows a certain amount of agreement between the two sites, even though the actual proportions are different (Fig. 14). There is, for instance, a trend in both areas towards a reduction in the restioid or 'grassy' element on the hillsides and a slight reduction in the amount of dense waterside vegetation. There is also some indication of an increase in open grassland on the flat ground. In addition, from about 8 000 B.P. there appears to have been an increase in dense vegetation on the lower hillsides in both areas.

It is interesting to note that in many cases the proportions of different species vary considerably in the modern samples from the Holocene samples. In general it is the species from the flat ground which are affected and it would thus appear that the differences are most probably due to the effects of agriculture. It has already been suggested that *Mus minutoides* is at an advantage in cultivated land, and it is here noticeable that relatively high proportions of this species distinguish all the modern samples. Reductions in the proportions of *Mystromys albicaudatus*, *Steatomys krebsi* and *Crocidura flavescens* could also be due to the destruction of their natural habitat by ploughing. Equally, the relatively high proportions of *Myosorex varius* and low proportions of *Otomys irroratus* could be due to the clearing of the valley floor at Boomplaas. At Byneskranskop, on the other hand, the habitat of these two species was not apparently altered. Also at Byneskranskop, the apparent replacement of the restioid or 'grassy' vegetation by scrub within the last 2 000 years is presumed to have been natural and, indeed, appears to have been a continuation of a trend. At Boomplaas, however, the situation seems to have remained stable during this period.

In this respect it is of interest to note that the evidence from *Crocidura flavescens* suggests that during approximately the last 4 000 years there has been a similar rise in temperature in both areas. The mean percentage difference between modern populations and those about 4 000 B.P. is 3,64 for Boomplaas and 2,57 for Byneskranskop (Table 35). It is possible, however, that the changes took place earlier at Boomplaas than at Byneskranskop, although there are insufficient data from BNK1 for this period to prove the point. It has, however, to be borne in mind that the mean difference of about 4,5 per cent between Byneskranskop and Boomplaas samples suggests a difference in temperature which could affect the time at which vegetational change took place in the two areas. This would, in fact, tend to suggest that changes at Byneskranskop were likely to have preceded those at Boomplaas because the temperature was higher in the former area. More data are clearly needed before the problem can be solved. This is especially the case since the diversity indices for Byneskranskop and Boomplaas are virtually identical, and it is clear that very similar conditions are indicated.

UPPER PLEISTOCENE AND MODERN SAMPLES

The factor analysis indicates that conditions during the central part of the M.S.A. occupation at Die Kelders 1 were very similar to those obtaining at

Boomplaas A during the period which has been interpreted as experiencing interstadial conditions. It is of some interest to note that the modern Congo valley samples also appear to represent similar conditions. The common denominator is a high proportion of *Myosorex varius*. Since it has already been suggested above that in modern samples this may be due to the effects of agriculture, it is thought that the correlation in the present case is probably largely spurious.

Conditions at Nelson Bay Cave at the time when levels YSL and YGL were deposited were quite different. This is to be expected because it is known that the last glacial maximum occurred at that time. This provides confirmation of the suggestion that there was a considerable difference between glacial maximum and interstadial conditions. At NBC there is evidence for open grassland on the flats, much as there is at the time of the lower M.S.A. levels at DK1, which may suggest relatively cold conditions at the latter site. It may also provide evidence for the known lower sea-level at NBC, as was suggested above for DK1. At NBC there is an indication of extensive restioid or 'grassy' vegetation which may perhaps have been situated on the land above the cave on what is now the coastal plain.

The evidence from *Crocidura flavescens* (Figs. 16–21, Tables 30–32) suggests that temperatures were very similar at NBC and at BPA during the last glacial maximum. This is of some interest in view of the fact that the later evidence from BNK1 suggests that there is a difference between the coast and the Congo valley. Also between DK1 and BPA, during what is thought to be an interstadial in the Last Glacial, there is evidence that temperatures were higher at DK1, which was presumably not far from the sea at the time. It may, therefore, be that at about 18 000 B.P., when the sea was about 80 km east of the site, NBC experienced a continental climate which was similar to that affecting the Congo valley. Subsequent raising of the sea-level would mean that a maritime climatic régime would have been reintroduced to the area of the present coast near Nelson Bay Cave. The fact that this would have the effect of moderating the climate could explain why there was apparently a differential rate of increase in temperature on the present coast and in the Congo valley. The mean percentage difference between the BPA sample and the BNK1 sample for the period about 13 000 B.P. is approximately double (9,57 per cent) that between the two samples for the period about 4 000 B.P. (4,41 per cent) (Table 35). This would suggest a relatively accelerated rate of temperature increase in the Congo valley during the time between the two dates, possibly in compensation for postulated earlier increases along the coast.

The general diversity indices for Nelson Bay Cave and the glacial maximum levels at Boomplaas A are very similar, although somewhat lower for the former. This again suggests that conditions were much the same in both areas. The diversity indices for Die Kelders 1 M.S.A. samples are also similar to those for samples thought to be approximately contemporary at Boomplaas A. The slightly higher results for DK1 would tend to confirm the suggestion that conditions were rather milder near this site than in the Congo valley.

EXISTING EVIDENCE FOR LATE QUATERNARY ENVIRONMENTS

In the present study the word 'environment' is used in the restricted sense of vegetation and climate. The latter, in turn, is represented by temperature and rainfall or, possibly, effective precipitation. This is because micro-mammalian evidence can provide information concerning the considerable changes which are known to have occurred in these particular aspects during the Upper Pleistocene and Holocene. Through assessment of the degree of difference from the present, taken as the norm, of these variables it is possible to establish a broad picture of past environments. However, what effect one parameter will have had on others is extremely difficult, if not impossible, to judge. This reflects both the complexity of the interrelationships of various aspects of the environment and the present state of knowledge on the subject. The result is that extrapolation from one aspect to another is a doubtful process, although necessary at times. However, by examining all the available evidence from different lines of research, interpretation may be based on as secure a foundation as possible. In this exercise it is preferable to move not only from the general to the particular but also from the complete to the incomplete. The data from deep-sea cores satisfy both requirements so that, as is argued by Kukla (1977), it would seem advisable to use these data as a base against which to measure terrestrial data. These latter have a tendency to be more localized in relevance but, at least in the more continuous sequences, general trends can be recognized and correlated with those in the deep-sea data. The geomorphological data tend to be both localized and incomplete and, as such, must be interpreted with particular care. They do, however, have undoubted importance for regional studies, especially when they can be fitted into the general framework. For the region currently under investigation, analysis of samples of terrestrial macrofauna from archaeological sites has also provided insight into past vegetational changes.

The basic framework of climatic change during approximately the last 125 000 years is well established. Different lines of evidence show that after being climatically similar to today, the remainder of the period was colder. After some oscillations the temperature dropped considerably about 75 000 B.P. A subsequent partial recovery was followed about 20 000 B.P. by the last maximum of the Last Glacial which is thought to have been the most severe. During this time temperatures in South Africa might have been up to 10 °C lower than at present on the interior plateau and high mountains, but were probably in the region of 5 °C lower in the coastal regions. There is also a possibility that there was less seasonal variability than at present. This climate appears to have been favourable to grass, which seems to have comprised a large part of the vegetation, at least on the coastal foreland and in intermontane valleys, during glacial periods.

From about 12 000 B.P. conditions began to improve rapidly. By about 8 000 B.P. a state approaching equilibrium seems to have been reached. Although it is clear that changes and fluctuations have continued to take place

they are obviously on a much smaller scale than those previously experienced. Both the oxygen-isotopic and the sea-level data indicate a reduction in the rate of change.

MARINE EVIDENCE

The evidence for palaeoclimatic change during the Upper Pleistocene and the Holocene from marine data has the advantage of being both essentially complete and basically comparable in all parts of the world. Evidence for changes in sea-level has long been studied, but the relatively recent advances in the interpretation of deep-sea cores have had a profound effect upon palaeoclimatic studies. These cores have the advantage of providing biotic and abiotic material for study which, amongst other things, allows cross-checking of results both from the cores themselves and from the sea-level data. In both cases oxygen-isotope analysis, which measures the amount of ^{18}O in calcareous foraminifera and thus the surrounding sea-water, is of great importance. Interpretation is based on the fact that during glacial periods not only is a larger proportion of the earth's water stored as ice at the poles, but also that ice is relatively low in ^{18}O . In compensation the oceans will be relatively high in ^{18}O at the same time and sea-levels will be lower. In this way the oxygen-isotope content of the water can be used to check whether contemporary low sea-levels are due to changes in ice volume or to isostatic uprising of the land mass.

Emiliani (1955, 1966) originally conducted oxygen-isotope analysis in order to establish a palaeotemperature sequence since he believed that changes in ^{18}O content were temperature dependent. He defined a climatic sequence in which, basically, the even-numbered stages represent glacial periods and the odd-numbered stages interglacial periods. Shackleton (1975) emphasizes, however, that these stages are related to the amount of ice present and not to the climates that caused the ice. Moreover, whilst the marine record is divided into roughly equal proportions of glacial and non-glacial time, there is evidence, particularly at high latitudes, that full interglacial conditions were of much shorter duration. Emiliani (1972) makes the point that periods when temperatures were as high as those of the present are exceptional and of short duration. Shackleton (1975) concludes that the oxygen-isotope stratigraphy provides a good framework but does not give sufficient information to allow specific interpretation on a regional basis. In this general framework stage 5 is correlated with the Last Interglacial, stage 3 with an interstadial in the Last Glacial and stage 1 with the Present Interglacial. The intervening stages 4 and 2 represent the first and last maxima of the Last Glacial. Subsequent work by Shackleton & Matthews (1977) has established the most reasonable time scale for stages 1 to 7 and a correlation with three high-sea-level terraces in Barbados. They conclude that Barbados III, the oldest and highest terrace, is dated to about 125 000 B.P. and is to be correlated with standard isotopic substage 5e, representing the Last Interglacial *sensu stricto*. Barbados II (105 000 B.P.) and I (82 000 B.P.), which also fall into stage 5, are thought to

owe their present elevation to uplift of the land so that Barbados III represents the last occasion when the continental ice-mass was as reduced as it is today. On the basis of ages given by Shackleton & Opdyke (1976), the first glacial maximum, stage 4, began about 75 000 B.P. and the last glacial maximum, stage 2, at about 32 000 B.P.

As was mentioned above, not only was the ocean water high in ^{18}O during glacial periods, but also the quantity of water was reduced. If the effect of tectonic and isostatic activity can be evaluated it should be possible to correlate evidence for higher or lower sea-levels with past climatic conditions, although differential rates of uplift can cause problems in interpretation. Problems also arise from the fact that evidence for lower sea-levels is frequently submerged, particularly for the Last Glacial when levels are generally thought to have been more than 100 m below those of the present (Truswell 1977) during the last maximum (Dingle & Rogers 1972). In southern Africa Butzer & Helgren (1972: 160) note evidence of a shoreline at +5–12 m which they believe pertains to the Last Interglacial, while Davies (1971, 1972) records evidence of such beaches all along the South African coast. The fact that the exact level varies could be due to differing local conditions or to the beaches having been formed during different stadia of the Last Interglacial. The evidence for low sea-levels comprises submerged sediments, usually on continental shelves, and drowned valleys and shorelines. Sediments laid down subaerially exist at several tens of metres on many shelves, especially off the eastern United States and western Europe, while drowned fluvial patterns off the coast of France have been discovered by the use of seismic plotting devices (Guilcher 1969: 83). In South Africa similar work has been carried out on the Agulhas Bank, where swathes of muddy sediment on the sea-floor are thought to indicate drowned river-valleys (Dingle & Rogers 1972: 162). Whether these pertain to the Last Glacial is perhaps more difficult to ascertain, although there would presumably be some evidence if they represented more than one period of low sea-level. Thereafter, during the Flandrian transgression, according to Shackleton & Opdyke (1973: 46), sea-level rose rapidly from about 16 000 B.P. to reach its present position some 6 000 years ago, although Montaggioni (1976) cites evidence from Réunion for a continuous rise in sea-level during the last 7 300 years to its present level. Butzer & Helgren (1972: 165) and Martin (1962: 25), on the other hand, follow Fairbridge (1961, 1971) in suggesting that the sea-level rose above its present level temporarily.

Faunal analyses of deep-sea cores have been based on changes in abundance of individual key species and, more recently, on considerations of the total fauna. As Shackleton (1975) has pointed out, the first method is too simple and has proved unreliable, particularly in the older samples. Analysis of all, or a large part, of the fauna represents a more sophisticated and reliable approach. Of particular interest appears to be the work of Imbrie & Kipp (1971) and Imbrie *et al.* (1973) which extracts quantitative estimates of surface water conditions from data of planktonic microfossils. Analysis of core tops,

that is the modern data, forms the basis against which the fossil samples are measured. Shackleton (1975) suggests that faunal analysis will prove useful for within-stage changes but not for between-stage changes. Imbrie *et al.* (1973) make the point, however, that oxygen-isotope analysis and their quantitative faunal analysis are complementary because they measure different local responses to global climatic change.

Luz (1973, 1977) used a modified version of the Imbrie *et al.* (1973) system to analyse the evidence from planktonic foraminifers in the Pacific Ocean. In the process he noticed (Luz 1977) a distinction between high-latitude faunal evidence and ^{18}O evidence from lower latitudes. His evidence from the south Pacific, the north Atlantic data of Sancetta *et al.* (1973), and the Camp Century (Greenland) ice-core data of Dansgaard *et al.* (1971) all indicate an initial sharp drop in temperature at about 75 000 B.P., followed by generally low temperatures during the remainder of the Last Glacial. In contrast, Luz (1977) notes a general decline, with fluctuations, in temperature in the ^{18}O record as discussed, for example, by Shackleton & Opdyke (1973). He is presumably right in intimating that latitude should not affect the evidence from oxygen-isotope analysis, although there may be some time lag in stabilization of oxygen-isotope ratios the further the position from the pole. Moreover, if the different analyses are measuring different responses this could have an effect. However, it would appear that, in fact, the differences may not be as great as is suggested. In the isotopic record there is also a relatively rapid drop in temperature, or increase in the polar ice mass, at the beginning of the Last Glacial. There is evidence for this in the Caribbean and the Pacific (Shackleton & Opdyke 1973). Thereafter Shackleton (1975) emphasizes that the establishment by Emiliani (1955) of stage 3 corresponding to an interstadial is easily recognizable in the oxygen-isotope record and that there is evidence for a climate significantly different from that of the preceding and succeeding maxima. The data given by Sancetta *et al.* (1973) also suggest a certain amount of recovery during the middle part of the Last Glacial. Where these data differ from those given by Shackleton & Opdyke (1973) is in suggesting that the first glacial maximum was as severe as the last. However, it is interesting to note that in his generalized temperature curve Emiliani (1972) shows precisely this situation. It would seem, therefore, that although the details vary, the overall pattern is the same. In terms of actual sea-surface temperature differences between glacial and interglacial maxima there is remarkable consistency, with a suggested 3 °C in the Caribbean (Shackleton & Opdyke 1973), 5 °C in the south Pacific (Luz 1977) and Emiliani's (1972) generalized curve showing an amplitude of about 6 °C. A similar situation off the shores of southern Africa is suggested. Vincent (1972) has used changes in the distribution pattern of planktonic foraminifers to postulate a 5 °C rise in temperature at about 10 000 B.P. where she recognizes the Pleistocene-Holocene boundary.

Hays *et al.* (1976), also using a version of the Imbrie *et al.* (1973) method, have created a reconstruction of the Atlantic and western Indian Ocean sectors

of the Antarctic Ocean at 18 000 B.P. One of the most notable features is that there is far less variation in the volume of sea-ice from summer to winter at 18 000 B.P. than there is today. This would presumably indicate less seasonal variability in climate. It is pointed out (Hays *et al.* 1976: 361) that there is effectively no temperature anomaly south of Africa with the position of the subtropical convergence and the Antarctic Polar Front being in substantially the same position then as now in this region. However, advance of the latter, particularly in the Atlantic, resulted in the constriction of the subantarctic zone with a consequent steepening of the thermal gradient. This will have had a wide effect, increasing winds and driving cold currents far north of their present positions. Likewise, increase in sea-ice will have steepened the thermal gradient to the equator, again causing stronger atmospheric circulation. There would also have been a general contraction of climatic zones towards the equator (Van Zinderen Bakker 1976) with the result that temperatures would have been considerably lower, due in particular to frequent influxes of very cold polar air in the winters. Moreover, Van Zinderen Bakker (1976) postulates higher rainfall resulting from an increase in the influence of the prevailing westerly winds. Bé & Duplessy (1976), on the other hand, provide evidence from both ^{18}O and faunal analysis to show that the subtropical convergence did, in fact, move northwards to 31°S in the Indian Ocean during the late Quaternary. This resulted in the weakening of the Agulhas Current so that the consequent cooling off the east coast of South Africa was greater than that off the west coast of Australia. Whether Hays *et al.* (1976) or Bé & Duplessy (1976) are correct, it is clear that, in both cases, the evidence is in general agreement with that from the oceans elsewhere in the world. It shows that considerably colder conditions existed off southern Africa during ^{18}O stages 2 and 4, that is, during the early and late pleniglacial of the Last Glacial.

TERRESTRIAL EVIDENCE

In a major attempt to correlate land and deep-sea data for past climatic fluctuations, Kukla (1977) has pointed out that serious miscorrelations have arisen from past failure to recognize that terrestrial records were incomplete. Insisting that only complete, or essentially complete, sequences can provide adequate information, Kukla (1977: 320) lists three types of land-based deposits which are likely to provide evidence comparable to the oceanic record. These are pollen-rich lake beds, continental ice-sheets and deposits of alternating loess and soils. Van der Hammen *et al.* (1971) have analysed pollen from the Netherlands and Macedonia to provide a detailed picture of vegetational and, by implication, climatic change during the late Cenozoic in Europe. Work by Woillard (1978*a*, 1978*b*) on the Grande Pile sequence in France provides evidence of glacial-interglacial cycles during the last 140 000 years which also emphasizes the complexity and number of climatic fluctuations occurring during that period. In both cases the evidence can be correlated with the deep-sea evidence (Kukla 1977: 319; Woillard 1978*a*: 12). Recent work in Norway

(Mangerud *et al.* 1979) has correlated the Eemian (Last) Interglacial with oxygen-isotope stage 5e by means of analysis of pollen and marine fossils.

Cores from the continental ice-sheets of both the Arctic and Antarctic have been examined (Dansgaard *et al.* 1971; Johnsen *et al.* 1972; Paterson *et al.* 1977). A history of temperature variation has been based on $\delta^{18}\text{O}$ in the ice. This is because the index is dependent on the air temperature at the time of deposition of the snow of which the ice is composed. There are, however, other factors influencing isotopic composition which cause Dansgaard *et al.* (1971: 37) to sound a cautionary note on direct interpretation. In particular there are problems connected with the interpretation of the Byrd Station, Antarctica, column (Johnsen *et al.* 1972). There is, however, good general correlation between the different ice-cores (Johnsen *et al.* 1972; Paterson *et al.* 1977), although they do not agree in all particulars. Dansgaard *et al.* (1971: 52) and Johnsen *et al.* (1972: 433) have attempted to correlate the evidence from Camp Century, Greenland, with accepted American and north European glacial terminology; Kukla (1977: 321) has correlated the Camp Century evidence with the Grande Pile evidence, thus providing the link between the two lines of evidence.

The loess evidence has been discussed in some detail by Kukla (1975, 1977). This evidence is particularly important because the essentially complete sequences can be correlated with the deep-sea evidence and with the classical glacial stages (Kukla 1977: 322). Palaeoclimatic information is forthcoming from analysis of the loess and interstratified soils and of their contained snail faunas. In permanently unglaciated areas such as central Europe, between the north European and Alpine glacial regions, a regular sequence of deposits was built up, with unvegetated loess accumulating during glacial periods and forested soils marking interglacial periods. The loess record has also shown that the palaeoclimatic record is far more complex than was suggested by the classical Alpine sequence which has normally been accepted. This record is, however, in good agreement with the deep-sea record (Kukla 1977: 365).

The general indication is that interglacial conditions, specifically the Last (Eemian) Interglacial, lasted from about 127 000 B.P. to about 105 000 B.P. This is correlated with oxygen-isotope stage 5e and the Barbados III high terrace. Cold intervals at about 105 000 B.P. and 90 000 B.P. (^{18}O stages 5d and 5b) interrupted a long, relatively warm period which lasted until about 73 000 B.P. (^{18}O stages 5c and 5a). This is correlated with Barbados II and I high terraces and the early glacial period of the Last (Würm or Weichselian) Glacial. The Amersfoort and Brørup interstadials of northern Europe can apparently be correlated with ^{18}O stages 5c and 5a respectively. The Camp Century ice-core can be correlated with these events and a third interstadial, equivalent to the Odderade of northern Europe, is also evident (Dansgaard *et al.* 1971: 52). The lower pleniglacial, which is shown by Van der Hammen *et al.* (1971: 394) to have begun about 60 000 B.P. but may have been earlier (see above), may be correlated with oxygen-isotope stage 4 and is apparent in the Camp Century core (at about 65 000 B.P.; Paterson *et al.* 1977: 511) as well as

the Grande Pile column. The middle pleniglacial, including the Moershoofd (50 000 B.P.), Hengelo (38 000 B.P.), and Denekamp (30 000 B.P.) interstadials (dates from Van der Hammen *et al.* 1971: 395) is recorded in the Netherlands pollen diagrams and can be correlated with ^{18}O stage 3. In general, this period is said to have been less cold and more humid than the preceding and succeeding periods (Van der Hammen *et al.* 1971; Kukla 1977: 365). The upper pleniglacial, ^{18}O stage 2, is well recorded in the pollen and ice-core sequences (Johnsen *et al.* 1972; Van der Hammen *et al.* 1971) as well as in the loess record (Kukla 1977: 330). The late glacial probably began about 14 000 to 13 000 B.P. (Van der Hammen *et al.* 1971: 396) with the Bølling interstadial at about 12 400 B.P. and the Allerød interstadial from about 11 800 to 10 900 B.P. The colder Older Dryas and Younger Dryas occurred between and after these interstadials, from 12 000 to 11 800 B.P. and 10 900 to 10 000 B.P. respectively. This represents the beginning of ^{18}O stage 1. Similar oscillations are visible in the loess and ice-core records. Thereafter, all lines of evidence show rapid amelioration of conditions and a return of interglacial climate and vegetation. There is some indication that the climate was warmer in the first half of the Holocene than the second (Dansgaard *et al.* 1971: 48) although the apparent evidence from the Netherlands is said to represent, in fact, the increasing destruction of forests by people (Van der Hammen *et al.* 1971: 396). The evidence from the Mediterranean (Tenaghi Philippon, eastern Macedonia) is perhaps of greater relevance for comparison with the southern Cape and it is, therefore, important to note that Van der Hammen *et al.* (1971: 394) have been able to correlate this sequence with that from the Netherlands.

The only potentially continuous terrestrial sequences from southern Africa come from pollen profiles. The first to be examined came from the interior of South Africa. At Florisbad (Van Zinderen Bakker 1957; Van Zinderen Bakker & Butzer 1973) the evidence suggests that very warm dry conditions with an increased Asteraceae element existed from some time before 40 000 B.P. At about 28 000 B.P. a series of oscillations from very arid to semi-arid warm conditions took place. From about 25 000 to 19 400 B.P. an increase in grass indicated a lower temperature, higher precipitation, or both. Livingstone (1975: 268) points out, however, that the ^{14}C dates are not internally consistent, so that the dating of the events is in some doubt. The profile from Aliwal North (Coetzee 1967; Van Zinderen Bakker & Butzer 1973) covers the period from about 12 600 B.P. to 10 000 B.P. and the observed oscillations have been correlated with the late glacial oscillations observed in Europe (Van Zinderen Bakker & Butzer 1973: 239). These fluctuations confirm the alternation of warm dry periods with cooler wetter periods, which was indicated for Florisbad. Recent work at Wonderkrater in the Transvaal (Scott & Vogel 1978) shows the same essential pattern during approximately the last 25 000 years. Here a transitional period, dated to 11 000–9 000 B.P., is correlated with the Aliwal North sequence and fluctuations in temperature and humidity are shown to have continued into the Holocene.

Of particular relevance to the southern Cape are two sequences which have been studied in some detail. The earlier of these comes from Rietvlei on the Cape Flats (Schalke 1973) and is said to cover the period from about 51 000 B.P. to the present, although the dating is insecure because of lying near the maximum range of the ^{14}C method. According to Schalke (1973) the middle pleniglacial is represented by five intervals, two of which are thought to have been wet and three dry. During the former, dated to approximately 45 000–40 500 B.P. and 36 500–33 000 B.P., a mixed *Podocarpus* forest resembling that of the Knysna region today is suggested for the central part of the Cape Flats. It is also suggested for the lower part of the upper pleniglacial in the region of 28 500 B.P. Thereafter evidence suggests dry conditions in the upper pleniglacial. During the dry phases and the Holocene, dune vegetation or coastal fynbos replaced the forest. Schalke (1973) explains the changes in terms of changes in humidity, whether due to increased rainfall or reduced evaporation. Van Zinderen Bakker (1976: 183) is of the opinion that the evidence has not been correctly interpreted. He points out, for instance, that except during the Salt River interval (45 000–40 500 B.P.) the evidence for forest in the region is not convincing (Van Zinderen Bakker 1976: 184) and even here the impression is that the forest was probably restricted to river margins and did not occur in the coastal area. There is, however, certainly evidence for change in the fynbos and grass cover as well as in the dune and marsh vegetation.

The evidence from Groenvlei (Martin 1968, 1969) covers the period from about 8 000 B.P. From then until about 7 000 B.P. the area appears to have been covered with a strong Asteraceae element. Tree pollen indicates a reduction in heath, perhaps by dunes, rather than an increase in forest. From about 6 800 B.P. until about 2 000 B.P. the forest element is reduced, which again could be due to sand or to a drier climate. Thereafter, first scrub and then forest spread quite rapidly, either because of the removal of the sand barrier or because of an increase in effective precipitation. It is thus not clear whether or not there were fluctuations in the climate, although amelioration does seem to have taken place at about 7 000 B.P. and again at about 2 000 B.P. At present Groenvlei is just within the western limit of the Knysna forest and it is possible that the evidence indicates, basically, the arrival of essentially modern conditions in that area at that time.

Auxiliary evidence from macrobotanical remains from archaeological sites is mostly confined to postglacial levels (Deacon 1972: 37) so that, as would be expected, modern vegetation patterns are mainly reflected. There are, however, some apparent differences. At Boomplaas A, for example, *Pappea capensis* fruits were found in levels dated to about 2 000 B.P.; this tree does not grow within a distance of 10 km of the site today (Moffett & Deacon 1977). Further evidence for vegetation changes at the end of the Pleistocene and through the Holocene in the foothills of the Swartberg Mountains is provided by the relative increase in the frequency of *Acacia karroo* charcoal found in archaeological sites (H. J. Deacon 1979 pers. comm.) There have been signi-

ficant changes in the dominant species in the woodland vegetation of this area and, notably, *A. karroo* has been able to extend its geographical range in the Holocene (H. J. Deacon 1979 pers. comm). This latter pattern is of wider significance (Acocks 1975: 8) and Deacon considers it to be related to dynamic adjustments in the distribution of individual taxa in response to warmer Holocene climates.

Geomorphological evidence provides further climatic data specific to southern Africa. Most particularly there is evidence for cold conditions during the Upper Pleistocene, partly because, as Flint has pointed out (1976), this evidence is more obvious and partly because most of the last 100 000 years appear to have been colder than the present. At high altitude in the Drakensberg Mountains and Lesotho periglacial phenomena indicate temperature drops of between 5.5°C and 9°C (Van Zinderen Bakker 1976) while oxygen-isotope work on speleothems in the central Transvaal (Talma *et al.* 1974) suggests a temperature 9°C lower than the present during the period 30 000–20 000 B.P. On the south coast, or the coastal foreland of the time, frost-fractured debris related to the Last Glacial has been described from Nelson Bay Cave (Butzer 1973; Butzer & Helgren 1972) and Die Kelders 1 (Tankard & Schweitzer 1974). A postulated temperature drop of 10°C (Butzer & Helgren 1972) to account for these phenomena is, however, perhaps excessive. Frequent very cold periods, as suggested by Van Zinderen Bakker (1976), could possibly have been responsible and would be more in keeping with the general evidence than an average drop of such a magnitude. Evidence for higher temperatures during the Holocene has been provided by isotopic analysis of molluscs from Nelson Bay Cave (Shackleton 1973).

As far as changes in relative humidity are concerned it would appear that the southern Cape was generally out of phase with the interior of South Africa (Van Zinderen Bakker & Butzer 1973; Butzer *et al.* 1978). Inland, as was also suggested by the pollen analyses, the evidence suggests wetter conditions during colder periods. At Alexandersfonteinpan Butzer *et al.* (1973) have postulated a rainfall approximately double that of the present at about 16 000 B.P., assuming a temperature depression of 6°C relative to that of the present. Along the Gaap Escarpment a subhumid climate is also postulated for the period 21 000 B.P. to 14 000 B.P. In the southern Cape, on the other hand, the indication is that during the period approximately 70 000 B.P. to 10 000 B.P. the climate was essentially dry (Butzer *et al.* 1978: 334). A wetter period is, however, inferred for the middle pleniglacial at Nelson Bay Cave (Butzer & Helgren 1972; Van Zinderen Bakker & Butzer 1973) and leaching of the Boomplaas A deposits after the last glacial maximum might have been due either to increased rainfall or to increased run-off (H. J. Deacon 1979 pers. comm.). Evidence for wetter conditions at Die Kelders 1 (Tankard & Schweitzer 1974) has not been dated but may also refer to the middle pleniglacial. Climatic change in southern Africa continued into the Holocene, as Butzer (1974) has pointed out. Butzer *et al.* (1978: 333) have divided the Holocene of

the southern Cape into three units. The early Holocene, up to about 4 200 B.P., was relatively dry with a more open vegetation than that of the present, and considerable aeolian activity. The period from 4 200 to 1 000 B.P. was apparently considerably wetter, with an increase in bush and forest. Thereafter, the effects of drier conditions were enhanced by increasing interference by man. The earlier Holocene was wetter in the interior but after about 4 000 B.P. the climate was similar to that of the coastal region. It is of some interest to note the suggestion by Mörner (1978) that changes in aridity may have been due, at least in part, to palaeogeoidal changes which would have altered the level of the ground-water table and not solely to climatic changes. Whatever the method responsible, it is perhaps likely that the resultant conditions would have been the same or similar. It need not, therefore, affect the type of qualitative or relative assessments of conditions being attempted here.

The macromammalian evidence from the southern Cape has provided a clear, although generalized, indication that during the Last Glacial the vegetation of the area must have been substantially different from that occurring in the Holocene and the recent past. Remains of large grazing antelope and zebra predominated in the glacial samples. Such species require relatively extensive open grassland; they were not and could not have been present in the southern Cape during the recent past. From this Klein (1972*a* etc.) has argued that during glacial times grass spread over much of the area. Under interglacial conditions the vegetation would have largely comprised scrub and bush, with forest in suitably watered and protected areas. The predominance of small browsing antelope in samples supposedly pre-dating the Last Glacial from Klasies River Mouth (Klein 1976) and from Boomplaas A (Klein 1978) as well as from the postglacial period from Byneskranskop 1 (Klein 1981) and Boomplaas A (Klein 1978) is taken as evidence for this change in vegetation. These trends would certainly be in keeping with those recorded in Europe, although fluctuations were apparently less extreme in southern Africa.

CORRELATION OF MICROMAMMALIAN AND EXISTING EVIDENCE

The general framework of climatic change during the last 125 000 years is well established, as has been discussed above. This framework is based upon quantitative data with wide application derived from more than one discipline of marine science. Micromammalian evidence currently provides non-quantitative data of restricted application. As such it must be placed within the general framework before it can realize its full potential. Whether or not it may be interpreted in terms of the framework also provides some test of its validity. Beyond this it is expected that the micromammalian data will provide more detailed regional information comparable with and complementary to that already available from other sources. In order to assess the contribution of the micromammalian evidence at this level it must be checked against that forthcoming from the geomorphology and palynology of the area. Comparison at an

even greater level of detail is made possible in the present case by the existence of macromammalian evidence from the same archaeological sites which have produced the micromammalian material being examined in this study.

GENERAL FRAMEWORK

The general framework consists of the ^{18}O stages of Emiliani (1955, 1966) which have found validity on a world-wide basis, as was discussed above. To this framework has been matched the major divisions of the last glacial cycle, based on work done in Europe. Within these divisions fluctuations or oscillations of lesser intensity or shorter duration have been identified for the northern hemisphere from various lines of evidence.

In the present section it is intended to show that the micromammalian evidence from the southern Cape correlates well with this general framework. Table 47 illustrates how the data from Boomplaas A, Byneskranskop 1 and Die Kelders 1 can be assigned to the ^{18}O stages and the major divisions of the glacial cycle. It is not to be expected that there will be any detailed agreement between southern African sequences and those from Europe. It is suggested, however, that a generally comparable series of events appears to have occurred in both areas.

The Boomplaas A evidence provides the clearest picture because the sequence is the longest. The precise position of the lowest levels cannot be

TABLE 47

Generalized correlation of palaeoenvironmental sequences for Boomplaas A, Byneskranskop 1, and Die Kelders 1 Middle Stone Age with ^{18}O stages and major divisions of the last glacial cycle.

¹⁸ O	last glacial cycle	BPA	BNK1	DK1MSA
1	present interglacial	unit 1	unit 1	
			unit 2	
			unit 3	
late glacial	unit 2			
—13 000 B.P. 2	upper pleniglacial	unit 3		unit 1
—32 000 B.P. 3	middle pleniglacial	unit 4		unit 2
—64 000 B.P. 4	lower pleniglacial	unit 5		unit 3
—75 000 B.P. 5a	early glacial			

See Tables 44–46 for details of palaeoenvironmental units.
Dates after Shackleton 1975.

ascertained at present, but it appears most likely that levels LOH and OCH represent part of ^{18}O stage 5a, the early glacial. This is because relatively mild conditions apparently pertained at the time and it seems probable that this can be correlated with the Odderade interstadial in Europe. Thereafter, the lower pleniglacial, ^{18}O stage 4, is represented by levels BOL5 up to BOL1. Palaeo-environmental unit 4 (Table 44) corresponds well with the middle pleniglacial, ^{18}O stage 3. Apparently warmer periods, such as at the time of levels BOL and BOL1 and again in levels BP2 and BP3, may possibly be comparable to the interstadials Moershoofd, Hengelo and Denekamp. Although it is not possible to be precise about the correlation, it is clear that fluctuations were occurring in the south which were very similar to those in the north. Moreover, Van der Hammen *et al.* (1971: 395) note that the climate of the middle pleniglacial was generally less cold and more humid than that of either the lower or the upper pleniglacial; the Boomplaas A micromammalian evidence indicates just this for the southern Cape. Palaeo-environmental unit 3 can be correlated with the upper pleniglacial, ^{18}O stage 2. The moderate conditions recorded for level BP1 may correspond to an interstadial at this time in the European sequence but, again, it is not possible to make any close correlation. Late glacial oscillations are well documented in Europe with the Bølling and Allerød interstadials alternating with the Older and Younger Dryas stadials. At Boomplaas A a period of amelioration in level CL, palaeo-environmental unit 2, represents the late glacial at the beginning of ^{18}O stage 1. This was followed by a period of fluctuation at the beginning of the Holocene, in level BRL, which may be part of the same phenomenon that occurred in Europe.

The Byneskranskop 1 sequence may be correlated with ^{18}O stage 1. It is almost entirely Holocene, but radiometric dating shows that some of the lowest levels were deposited during the Upper Pleistocene. The micromammalian evidence (Table 45) suggests that levels 19 and 18 may be divided off in this way and represent the late glacial. A certain amount of fluctuation, but of lesser intensity, was apparent within the Holocene sequence here as it was at Boomplaas A. This, however, will be discussed in the next section.

The evidence from much of the Die Kelders 1 M.S.A. sequence suggests moderate conditions, as was discussed above. It would seem that palaeo-environmental unit 3 (Table 46), comprising the period covered by levels 14 up to 12, represents the last part of the lower pleniglacial, ^{18}O stage 4. Palaeo-environmental unit 2, the period covered by levels 11 up to 3, appears to be correlated with the middle pleniglacial, ^{18}O stage 3. The beginning of the upper pleniglacial, ^{18}O stage 2, is then probably represented by palaeo-environmental unit 1 but the site apparently ceased to be occupied before the last glacial maximum. The suggestion that the micromammalian evidence indicates lower sea-levels in the lowermost and uppermost levels than in the central levels would be in accordance with this general division. The top two levels may indicate the same interstadial conditions as those perhaps represented by samples from Boomplaas A levels BP3 and BP2 but, as was pointed out above,

it is not possible to make good correlations with the European interstadials of this period.

SOUTHERN AFRICAN EVIDENCE

It has been pointed out that the evidence suggests that climatic changes in the southern Cape were different from those in the interior of South Africa (Butzer *et al.* 1978). This is perhaps not unexpected in view of the modern situation where the climate is different in the two areas. However, although different in direction, the changes tend to have been contemporary, which, again, may be expected. The micromammalian evidence shows some agreement with the timing of change as indicated by the palynological evidence. It also tends to support other evidence for southern Cape conditions.

It would appear that it is not really possible to compare the climatic evidence from the Rietvlei palynological sequence with that from the micromammalian data for Boomplaas A. The resolution is different in the two cases and the dating, being near the limits of the radiocarbon range, is correspondingly uncertain. It may be that the drier Milnerton interval could be correlated with BPA level BOL, but there appears to be no correlation between the drier Killarney interval and the evidence from the middle pleniglacial levels at Boomplaas A.

At Byneskranskop 1 the evidence suggests that the period from about 6 400 B.P. to 3 900 B.P. was relatively dry. This agrees with the evidence for Groenvlei for the second half of the Holocene; it is harder to reconcile the evidence for the first half, although it is possible that the Boomplaas A evidence is in agreement. Possibly the difference between the suggested climate before and after 6 500 B.P. at Byneskranskop 1 is not great. Equally, it has to be borne in mind that the estimations are relative and it is difficult, on present evidence, to know what this would mean in absolute terms. It is also possible that an adjustment may need to be made to the micromammalian interpretation, but this will have to await further data.

The types of vegetation which have been shown to have occurred on the Cape Flats and at Groenvlei cannot be shown to have existed in the vicinity of the archaeological sites. This is not unexpected, however, since the vegetation is different today and the precise form of the vegetation tends, in any case, to be very regional due to its response to differing conditions. It may ultimately become possible to postulate what would be the equivalent vegetation for different areas under different climates, but for the present there are insufficient data.

The geomorphological data provide evidence for changes in both temperature and humidity. As was mentioned, data concerning the former generally indicate colder conditions. The micromammalian evidence from Boomplaas A and Nelson Bay Cave gives convincing support for the other evidence for cold conditions during the upper pleniglacial, especially the last glacial maximum. There does not appear to be other evidence for a cold climate during the lower

pleniglacial, except that forthcoming from Die Kelders 1 which Tankard & Schweitzer (1974) have recorded. The micromammalian evidence tends, however, to suggest that the period of maximum cold in the lower pleniglacial was not represented at this site. It is difficult, on the basis of present evidence, to reconcile this with the presence of *éboulis secs* in levels 12 up to 10. The wetter conditions indicated for the middle pleniglacial at Nelson Bay Cave, and probably Die Kelders 1, are also suggested for the Cango valley at that time by the micromammalian evidence from Boomplaas A. There is, however, no micromammalian evidence to compare with the geomorphological evidence from Boomplaas A for wet conditions at the end of the upper pleniglacial. Possibly these were caused by an increase in rainfall preceding the increase in temperature during the late glacial and it may be that the situation existed for a short period and, thus, did not affect the micromammals. Possibly, also, increased run-off rather than increased precipitation could cause the pronounced leaching (H. J. Deacon 1978 pers. comm.) but not influence the micromammalian species. The geomorphological and palynological evidence for the Holocene has been correlated by Butzer *et al.* (1978). The remarks above in reference to the palynological evidence may, therefore, be taken as applying equally to the geomorphological data.

MACROMAMMALIAN EVIDENCE

Comparison at the most detailed level may be made with the evidence from macromammalian material examined by Klein (1972 *et seq.*) from the sites which are discussed in this study. Klein's pioneering work has been hampered by small minimum numbers and by a lack of comparative data from other lines of investigation; for this reason he has been obliged to restrict his palaeoenvironmental interpretation of the data to general statements (Klein 1972*b*, 1976, 1978, 1981). The problem of numbers remains, of course, but now there are comparative data from the small mammal evidence. It is, therefore, possible to examine the macromammalian evidence from a different angle and perhaps to provide complementary confirmation of the interpretation of the two sets of data, thereby strengthening the validity of faunal investigations for palaeoenvironmental reconstruction.

It is not appropriate here to consider in any detail the problems connected with macromammalian samples and their interpretation. Many of the considerations discussed above apply equally to macromammalian evidence and may be considered in this connection. It is, however, necessary to mention a few points which could have a direct bearing on the interpretation of the present samples. In the first place, because the samples are small it is particularly relevant to bear in mind that the absence of certain species may well be due to the smallness of the sample rather than to changes in the environment. The composition of the sample will almost certainly have been biased by selection on the part of the people whose food debris the sample represents. Moreover, there is the possibility that hunter and prey may not have occurred

together in a particular area at a given time. In other words, if the game animal is migratory and the hunter moves seasonally between the coast and inland, as is suggested by Parkington (1972, 1976) for the west coast and has been documented orally for the south coast (Deacon 1969: 163), it is possible that man and animal could both visit the same place but at different times. While it is perhaps unlikely that an efficient group of hunter-gatherers would know so little about game movements as to allow this to happen, there remains always the possibility that these people could have chosen deliberately not to have hunted certain animals.

Interpretation will undoubtedly become more refined when it is possible to identify the high proportions of presently unidentified bovid material from Boomplaas A (Klein 1978), Byneskranskop 1 (Klein 1981) and Die Kelders 1 M.S.A. levels (Klein unpublished). It is unfortunate that this material cannot be used for interpretation at present because the groupings do not coincide sufficiently closely with usable ecological groupings such as those of Jarman (1974). Meanwhile, it is clearly necessary to group the samples of identified material in order to obtain adequate numbers in the samples. Klein (1972b, 1976, 1978, 1981) has been obliged to group the samples according to culture-stratigraphic units because he had no other basis for division. This has the unfortunate effect of forcing cultural change to coincide with environmental change. The micromammalian evidence suggests, in fact, that this close correlation is fallacious. For this reason, and in order to facilitate comparison, Klein's data were regrouped according to divisions indicated by the micromammalian evidence. This exercise does not invalidate the general conclusions reached by Klein but does allow a different approach to a more detailed interpretation. It is clear, however, that grouping on this scale, whatever the basis, obscures many realities of change and that there can be no substitute for adequate samples as a prerequisite for reliable interpretation.

Boomplaas A

Table 48 gives the data for perissodactyls and artiodactyls from Boomplaas A, grouped as nearly as possible in accordance with the micromammalian divisions (Table 44). As Klein (1978: 68) has pointed out, the samples for the lower half of the sequence are very small so that, until the full sample has been analysed, the evidence is uncertain. Klein (1978: 68) has suggested that the Last Interglacial is represented in the lowest levels, with a high incidence of smaller bovids suggesting closed vegetation similar to that of the Holocene and the present. He further suggested that the evidence indicates an expansion of grass during the last glacial maximum and then a gradual closing of the vegetation during the late glacial and into the Holocene.

In an area such as the Congo valley where there is complex topography, it is necessary to determine where individual species are to be found. In the macrofauna there are four species that are likely to occur on the hillsides rather than on the valley floor. *Tragelaphus strepsiceros* (greater kudu), *Redunca*

TABLE 48

Percentage representation of perissodactyls and artiodactyls at Boomplaas A (based on data in Klein 1978).

	DGL	BLD3	BLA	BRL	CL	GWA-YOL	BP-OLP	BOL-LOH
PERISSODACTYLA								
? <i>Diceros bicornis</i>	0,94	—	—	—	—	—	—	—
<i>Equus capensis</i> *	—	—	—	—	2,08	0,88	—	—
<i>Equus zebra/quagga</i> *	4,72	3,45	4,88	4,46	9,38	6,19	—	2,78
ARTIODACTYLA								
<i>Potamochoerus porcus</i>	—	—	—	0,89	—	—	—	—
<i>Phacochoerus aethiopicus</i>	—	—	—	—	0,52	—	—	—
Suidae indet.	0,94	1,72	—	0,89	0,52	—	—	—
<i>Pelorovis antiquus</i> *	—	—	—	—	1,04	1,77	—	—
<i>Syncerus caffer</i>	—	1,72	—	—	2,08	1,77	—	—
<i>Tragelaphus strepsiceros</i>	—	—	—	0,89	0,52	—	—	—
<i>Taurotragus oryx</i>	—	—	—	3,57	8,33	2,65	—	—
<i>Redunca arundinum</i>	—	—	—	0,45	—	—	—	—
<i>Redunca fulvorufa</i>	—	—	—	1,79	1,56	—	—	—
<i>Hippotragus leucophaeus</i> */ <i>equinus</i>	0,94	13,79	12,20	1,79	5,21	3,54	—	—
<i>Connochaeetes gnomi</i> /Alcelaphus	—	—	2,44	—	—	—	—	—
<i>buselaphus caania</i>	—	5,17	2,44	9,38	16,15	17,70	28,57	5,56
<i>Megalotragus priscus</i> *	—	—	—	—	—	0,88	—	—
Alcelaphini indet.	—	—	—	—	—	5,31	—	—
<i>Damalisca niro</i> */ <i>lorcas</i>	—	—	—	0,89	1,04	2,65	—	—
<i>Anidorcas</i> sp.	—	—	—	—	1,04	1,77	—	2,78
<i>Oreotragus oreotragus</i>	4,72	8,62	9,76	11,16	1,04	4,42	—	—
<i>Raphicerus campestris/melanotis</i>	7,55	12,07	14,63	9,82	2,60	0,88	4,76	19,44
<i>Pelea capreolus</i>	0,94	—	2,44	4,91	2,08	1,77	—	11,11
<i>Ovis aries</i>	16,04	1,72	—	—	—	—	—	—
Bovidae indet. — small	32,08	25,86	24,39	21,43	5,21	6,19	23,81	19,44
small medium	27,36	15,52	14,63	7,59	4,69	5,31	19,05	27,78
large medium	3,77	6,90	9,76	15,18	22,40	29,20	23,81	11,11
large	—	3,45	2,44	4,91	12,50	7,08	—	—
	N =	106	58	41	224	192	113	36

*Extinct species

fulvorufula (mountain reedbuck), *Pelea capreolus* (grey rhebuck or vaal ribbok), and *Oreotragus oreotragus* (klipspringer) all occur in rocky or hilly country (Ferrar & Walker 1974: 142; Jarman 1974: app. 1), although the first is not confined to it (Bigalke 1978: 1028). If the *Equus* species were *E. zebra* (mountain zebra) it would also have occurred in rocky mountainous terrain (Bigalke 1978: 1019). The remaining species were probably to be found on the valley floor, or, perhaps, on gentler slopes such as are found near the head of the valley. It seems, therefore, that the majority of the evidence refers to this area which does not constitute a very high proportion of the ground in the vicinity of Boomplaas A. Nearer the top of the valley, where the terrain becomes less rugged, it may have provided a larger acceptable habitat for those species normally to be found on plains. It has, of course, always to be borne in mind that the numbers of individuals represented in the samples need not suggest large herds, especially considering the long, or relatively long, periods of time represented. The micromammalian evidence suggests that there was always some grass on the valley floor, so that there might have been other reasons for the changing composition of the macromammalian fauna.

There is undoubtedly a high proportion of *Raphicerus* spp. in the lowest levels and their distribution within these levels follows closely the suggested climatic fluctuations given in Table 44. It is possible, therefore, that the evidence could indicate interstadial conditions rather than full interglacial conditions. From this point of view it is notable that the total proportions of small bovids (*sensu* Klein 1978) in the lowest levels is rather lower than that in the Holocene levels, which would suggest that the situation was not entirely the same in both periods. It would, of course, also assist interpretation if the two species of *Raphicerus* could be distinguished. The presence of *Alcelaphus buselaphus caama* (red hartebeest) or *Connochaetes gnou* (black wildebeest) suggests fairly open grass or open mesic grassland or shrubs, with some trees in the case of the former (Bigalke 1978: 1035; pers. comm.). *Antidorcas marsupialis* (springbok) generally occurs in drier country with open, short grass or shrubs (Bigalke 1978: 1025) but also makes some use of mesic grassland (R. C. Bigalke 1979 pers. comm.). *Pelea capreolus* indicates short, open shrubby or grassy vegetation on the hills (Bigalke 1978: 1030). This does not disagree with the micromammalian evidence, and the apparent openness of the vegetation is consistent with the suggestion that a glacial maximum occurred during the time the BOL levels were accumulated.

The large mammal evidence tends to confirm the suggestion that the material from OLP and BP levels indicates intermediate conditions. The evidence is very slight but proportions of small and small medium bovids are both intermediate. The high proportions of *Alcelaphus buselaphus caama* or *Connochaetes gnou* are interesting and suggest that mesic conditions with open grass or shrubs prevailed.

It may be possible that the preponderance of large medium bovids during the glacial maximum is due to their having sought refuge either from the

extremes of temperature or from reduced grazing in the Little Karoo at that time. If the Congo valley is considered as a refugium, it need not necessarily mean that there was a great change in the vegetation as it affected these species. In fact, the indication would be that less change occurred in the Congo valley than in less sheltered places. Moreover, the low numbers of large bovids involved (Klein 1978) would not have required extensive grass for their sustenance. The reduction in the proportion of *Raphicerus* spp. would then result from improved availability of the larger species. The presence of *Syncerus caffer* (buffalo) indicates that there remained a certain amount of dense vegetation during this period, as was also suggested by the micromammalian evidence. Some endorsement of the hypothesis of apparent rather than real change is provided by the hillside species which show a different pattern of representation. *Equus* sp. (assuming *E. zebra*), *Pelea capreolus* and *Oreotragus oreotragus* all occur in approximately the same proportions during the glacial maximum (upper pleniglacial) as they do during the later Holocene (DGL unit). These species are not migratory (Jarman 1974) and may be taken as indicative of prevailing conditions near the site during the periods under consideration. According to this evidence there was little difference in vegetation during the two periods. If the hillside species are unable to reflect change it could be argued that the changes in the valley floor species cannot be a simple reflection of vegetational change at this site.

The beginning of a reduction in proportions of open-country species such as *Alcelaphus buselaphus caama* or *Connochaetes gnou* and *Antidorcas* sp. in the late glacial (CL unit) can presumably be taken as indicative of a reverse migration of these species back to the Little Karoo as conditions ameliorated. Although there is a proportional reduction in these species, there is an increase in actual numbers of individuals represented and it may be that milder conditions caused overcrowding which initiated the move out of the valley. At the same time an increase in *Taurotragus oryx* (eland) and of *Syncerus caffer* may perhaps be taken as indicative of an increase in forbs and shrubs in the first instance and of riverine bush in the second instance. This latter situation may account for an increase in *Hippotragus* spp. which tend to need more cover (Bigalke 1978: 1033). Both would be consistent with the micromammalian evidence. It is interesting to note in this context that *Tragelaphus strepsiceros* has so far been recovered only from deposits of this age and those next youngest. The presence of this species indicates thickets and other dense shrubby vegetation, probably on the hillsides. In general the macromammalian evidence for this period gives a rather less clear indication of the intermediate nature of conditions than do the micromammalian data, but it is still present and thus confirms the pattern.

In the BRL unit Holocene conditions are shown by both sets of data to have become established. There is continued reduction or disappearance of the open-country forms (*Alcelaphus buselaphus caama* or *Connochaetes gnou* and *Antidorcas* sp.). There appears to have been a higher than usual emphasis on

hillside species from this time, at least until about 2 000 B.P. and possibly after this. This phenomenon is probably connected with the mechanics of acquiring food rather than with palaeoenvironmental change. Thus, if it is accepted that large gregarious animals, which have non-concealing habits in an open habitat (Estes 1971: 174), are potentially easier to find and kill than small solitary animals, which have concealing habits in a closed habitat (Estes 1971: 174), and also offer a better return for expended effort, then it is likely that as the larger species disappear the hunters will turn to the next largest available species. In this case this happens to be the hillside species. If this argument is correct, it would suggest that in general changing proportions of the larger species may reflect real changes in availability of species; the smaller the species the more likely it is to be present throughout the period, and apparent changes in its proportion to reflect only availability of the larger species. This would perhaps not affect the overall interpretation, but it is important to bear in mind the presence of such potential biases in the samples.

Byneskranskop 1

Table 49 gives the percentage representation of perissodactyls and artiodactyls in the Byneskranskop 1 samples, grouped according to the results of the micromammalian analysis. It is clear in overall terms that the larger ruminants tend to predominate in the lower half of the sequence and the smaller ruminants in the upper half, as Klein (1981) has pointed out. This change had been taken as indicative of the replacement of extensive grass by a more bushy vegetation (Klein 1981). Closer examination of the evidence suggests that both the large and the small mammal data provide a very similar indication of past environmental change. It is noticeable, for instance, that both *Taurotragus oryx* (eland) (although not positively identified from the upper levels) and *Syncerus* cf. *caffer* (buffalo), together with the undetermined 'large bovid' category, occur in approximately equal proportions in all three time periods recognized. In the case of the first species this may be because it has very wide habitat tolerance (Bigalke 1978: 1030), grazes and browses (Hofmann & Stewart 1972: 236) and can do without water (Bigalke 1978: 1030). This would suggest that it would be impervious to relatively minor environmental changes. *S. caffer*, on the other hand, prefers dense vegetation, being essentially a woodland species (Lamprey 1963: 76), and is a fresh-grass grazer dependent upon water (Hofmann & Stewart 1972: 231). The riverine vegetation, which is present throughout according to the micromammalian evidence also, could presumably have proved a suitable habitat during the period under discussion. The presence of this species in the area does, however, also indicate that there was grass at all times, as is indicated by the micromammalian evidence.

Of the species which were more numerous in the lower levels, the majority seems to have been dependent upon surface water and this may be taken as confirmation that this period was relatively wet, as is suggested by the micromammalian evidence (Table 45). Apart from *Diceros bicornis* (black rhino-

TABLE 49

Percentage representation of perissodactyls and artiodactyls at Byneskranskop 1 (based on unpublished data, courtesy of R. G. Klein).

	1-4	5-10	11-19
PERISSODACTYLA			
<i>Diceros bicornis</i>	—	0,84	1,33
Rhinocerotidae indet.	0,68	1,68	3,11
<i>Equus</i> cf. <i>capensis</i> *	—	—	0,44
<i>Equus</i> cf. <i>quagga</i> *	—	0,42	4,89
ARTIODACTYLA			
<i>Potamochoerus porcus</i>	4,79	2,52	1,33
<i>Phacochoerus aethiopicus</i>	—	—	0,44
Suidae indet.	4,79	2,94	4,00
<i>Hippopotamus amphibius</i>	0,68	1,26	0,44
<i>Syncerus caffer</i>	6,85	7,56	4,89
<i>Taurotragus oryx</i>	—	0,84	2,22
<i>Redunca arundinum</i>	—	0,84	2,67
<i>Redunca fulvorufula</i>	0,68	—	1,33
<i>Hippotragus</i> spp.	0,68	2,52	4,89
<i>Connochaetes</i> sp./ <i>Alcelaphus</i> sp.	2,74	2,10	11,11
<i>Damaliscus dorcas</i>	—	—	2,22
<i>Oreotragus oreotragus</i>	2,05	1,68	1,33
<i>Raphicerus campestris</i>	2,74	0,84	—
<i>Raphicerus melanotis</i>	6,16	8,82	1,33
<i>Raphicerus</i> spp.	17,12	22,27	8,00
<i>Pelea capreolus</i>	0,68	0,84	0,44
<i>Ovis aries</i>	7,53	—	—
Bovidae indet.—small	19,86	23,95	10,67
small medium	10,27	2,94	4,44
large medium	4,11	5,46	20,89
large	7,53	9,66	7,56
N =	146	238	225

See Table 48 for English common names.

* Extinct species.

ceros), which is said to prefer fairly dense vegetation (Bigalke 1978: 1018) but is certainly not restricted to it (personal observation), these species appear to have a preference for open grassland (*Equus* cf. *quagga* (quagga), *Damaliscus dorcas dorcas* (bontebok), *Connochaetes* spp. (wildebeest) or possibly open savanna (*Alcelaphus buselaphus caama* (red hartebeest), *Hippotragus leucophaeus* (blue antelope) (Klein 1974b: 113)). *Redunca arundinum* (reedbuck) indicates taller, denser grass (Ferrar & Walker 1974: 143). This evidence agrees with that from the microfauna which indicates that, apart from extensive grass on the plains, there was probably a considerable amount of dense vegetation along the river and between the river and Byneskranskop itself. *Redunca fulvorufula* (mountain reedbuck) and *Oreotragus oreotragus* (klipspringer) suggest the presence of both grass and shrubs on the hills which, again, is in keeping with the micromammalian evidence. The occurrence of *Phacochoerus*

aethiopicus (wart-hog), although represented by only one individual, is consistent with the general picture, since it is an open woodland species (Lamprey 1963: 76) with a preference for abundant vegetation including short grass (Hirst 1975: 40). Superficially the later increase in *Potamochoerus porcus* (bush-pig), which is indicative of closed bush (Bigalke 1978: 1019), would appear to contradict the suggestion of wetter conditions during the earlier period. It may, however, be as Klein suggested (1976: 83), that the earlier people were disinclined to hunt pigs, which have a reputation for ferocity, although it is perhaps doubtful whether they can have been harder to catch than *Diceros bicornis*. Both could, in any case, have been scavenged—which would negate the argument. It would seem that from about 6 500 B.P. conditions remained essentially the same until the site was abandoned. This is not entirely in agreement with the micromammalian evidence, but it is possible that minor fluctuations have been reflected by the latter which would not have affected the macromammals.

Die Kelders 1 Middle Stone Age samples

Table 50 gives the percentage representation of perissodactyl and artiodactyl species in the samples from the M.S.A. levels at Die Kelders 1, grouped according to the micromammalian evidence. Klein (1975: 265) has pointed out that large bovids are not well represented in these samples. The high proportion of small bovids would appear to agree with the suggestion that interpleni-glacial conditions pertained, especially during the central period. There appear, however, to be contradictions which cannot be readily explained. *Connochaetes* sp. (wildebeest) occurs in rather higher proportions in the upper and lower levels, but *Hippotragus leucophaeus* (blue antelope) and *Damaliscus* sp. (har-tebeest) occur only in the middle levels. Possibly *Hippotragus leucophaeus* indicates that there were some trees during the central period but not during the earlier and later periods; the significance of the other two genera may depend upon which species is represented. *Syncerus caffer* (buffalo) occurs only in the middle levels but *?Diceros bicornis* (black rhinoceros) occurs in higher proportions in the upper and lower levels, despite the fact that both species have a preference for fairly dense vegetation (Lamprey 1963). There are, however, at least two differences; *Syncerus caffer* is a migratory grazer (Jarman 1974: 223; Hofmann & Stewart 1972: 231) whereas *D. bicornis* is a sedentary browser (Lamprey 1963: 77). It is possible that suitable grass was available for *S. caffer* only during the central period, or that its visits to the vicinity of Die Kelders 1 coincided with those of the people only during that time, or that the earlier and later samples are too small to include this species. The increase in *Tragelaphus strepsiceros* (greater kudu) and in *?Pelea capreolus* (grey rhebuck) in the upper levels can probably be accepted as endorsing the micromammalian evidence for increased scrub on the hillsides during this period on the basis of the ecological data given by Ferrar & Walker (1974: 142) and Bigalke (1978: 1030). *Redunca fulvorufula* (mountain reedbuck) may, on the other hand,

TABLE 50

Percentage representation of perissodactyls and artiodactyls in Die Kelders 1 Middle Stone Age levels (based on unpublished data, courtesy of R. G. Klein).

	1-2	3-11	12-14
PERISSODACTYLA			
<i>?Diceros bicornis</i>	2,78	1,16	2,78
<i>Equus cf. quagga</i> *	—	0,29	—
ARTIODACTYLA			
<i>Hippopotamus amphibius</i>	1,39	1,74	2,78
<i>Pelorovis antiquus</i> *	1,39	0,87	—
<i>Syncerus caffer</i>	—	1,16	—
<i>Tragelaphus strepsiceros</i>	1,39	0,58	—
<i>Taurotragus oryx</i>	8,33	4,93	13,89
<i>Redunca arundinum</i>	1,39	1,45	—
<i>Redunca fulvorufula</i>	—	0,29	—
<i>Hippotragus leucophaeus</i> *	—	1,74	—
<i>Connochaetes</i> sp.	2,78	1,45	2,78
<i>Damaliscus</i> sp.	—	0,29	—
<i>Antidorcas cf. australis</i> *	2,78	1,45	—
<i>Oreotragus oreotragus</i>	2,78	3,48	2,78
<i>Raphicerus melanotis</i>	16,67	33,04	16,67
<i>?Pelea capreolus</i>	6,94	4,06	—
Bovidae indet.—small	22,22	20,87	27,78
small medium	11,11	6,38	5,56
large medium	1,39	4,93	5,56
large	5,56	2,90	5,56
very large	11,11	6,96	13,89
N =	72	345	36

See Table 48 for English common names.

* Extinct species.

suggest tall grass with shrubs on the hillsides (Bigalke 1978: 1031) during the central period. Bigalke (1978: 1031) notes that this species is to be found in more arid areas. This is interesting in view of the fact that the only specimen from Die Kelders 1 M.S.A. levels was recovered from level 3, one of the levels which it is tentatively suggested, on the basis of the micromammalian evidence, might have been deposited at a time of a fairly dry climate.

In general, the micromammalian and macromammalian evidence is in accord for this site, even to the extent that both sets of data suggest complications in the interpretation. The basic picture is reasonably clear but it would seem that clarification of the details will have to await the acquisition of a longer sequence with which the Die Kelders 1 sequence may be compared, or more information on the species, or both.

MICROMAMMALIAN EVIDENCE FOR SITE CORRELATION

As a corollary to the main study the use of micromammalian evidence to suggest generalized correlations of undated or insecurely dated sites was investigated. Unlike biostratigraphies which require that stages in the evolution

of various species be matched at different sites, the present correlations are based upon changes in community composition and, therefore, upon environmental change. It may also be possible to indicate approximate dates by comparison of the micromammalian evidence with that from other lines of research. Thus a base date for Boomplaas A may be suggested and, within broad limits, dates for the M.S.A. occupation of Die Kelders 1, after this site has been correlated with Boomplaas A. Such exercises are not generally useful for Holocene sequences because it is normally possible to acquire good ^{14}C dates which preclude the need for indirect methods of dating.

Of the Upper Pleistocene sites in the southern Cape, only two have thus far provided a sequence of micromammalian samples sufficiently long and complete to afford the possibility of correlation on this basis. The Boomplaas A sequence is absolutely dated to the limits of ^{14}C dating, but the length of the period of occupation prior to this can only be estimated. At Die Kelders 1 no reliable dates have been obtained for the M.S.A. levels. The fact that these are separated from the dated L.S.A. levels by deposits representing an unknown period of time when the site was not occupied, means that neither the date nor the duration of the M.S.A. occupation is known. Tankard & Schweitzer (1974) have, however, suggested on geological grounds that the period of occupation was from about 80 000 B.P. to 35 000 B.P. Deacon (1979) considers that the base of the Boomplaas A sequence may be dated to about 80 000 B.P., while Klein (1978) has suggested, on the macromammalian evidence, that the date may be nearer 100 000 B.P.

The micromammalian evidence tends to support the suggestion (Deacon 1979) that the age of the earliest deposits at Boomplaas A is approximately 80 000 B.P. As was mentioned above, it appears most likely that levels LOH and OCH were deposited during the early glacial period which lasted until perhaps 70 000 B.P. The micromammalian evidence suggests that in these two levels intermediate conditions are represented, and it is perhaps possible to equate these with the Odderade interstadial at the end of the early glacial in northern Europe or ^{18}O stage 5a which is characterized as relatively warm. Such evidence is not, in fact, inconsistent with that from the macromammals (Klein 1978). It is possible that conditions during all the warmer intervals of ^{18}O stage 5 were sufficiently similar to those of the Holocene not to be differently represented in the macromammalian evidence. It would be possible for this evidence to refer to a later rather than an earlier warm interval.

Variation in percentage of total variance accounted for by factors in the analysis of Upper Pleistocene levels at various sites and changing representation of different species (Fig. 32) indicate a possible correlation between Boomplaas A and the M.S.A. levels at Die Kelders 1. It is not suggested that the actual proportions of species are the same at both sites or that factors explain the same amount of variance at both sites. It is, however, suggested that changes of proportion and amount of variance within each site display similar patterns at the two sites. On this basis it would appear that the Die

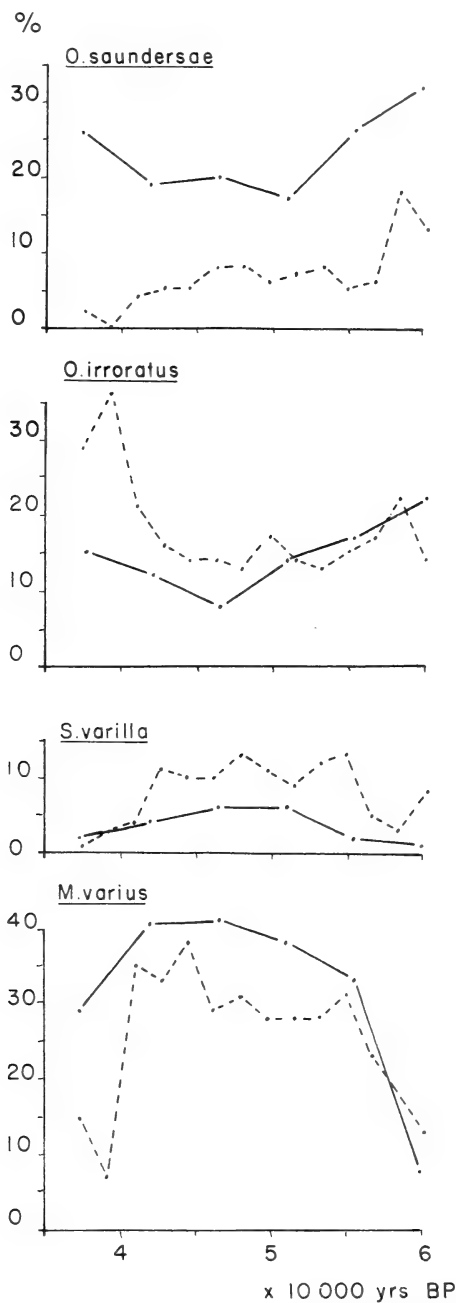


Fig. 32. First alternative correlation of the Boomplaas A and Die Kelders 1 M.S.A. sequences. BPA levels OLP to BOL1-3 and the DK1 M.S.A. sequence correlated using individual species. (Solid line = Boomplaas A; dashed line = Die Kelders 1.)

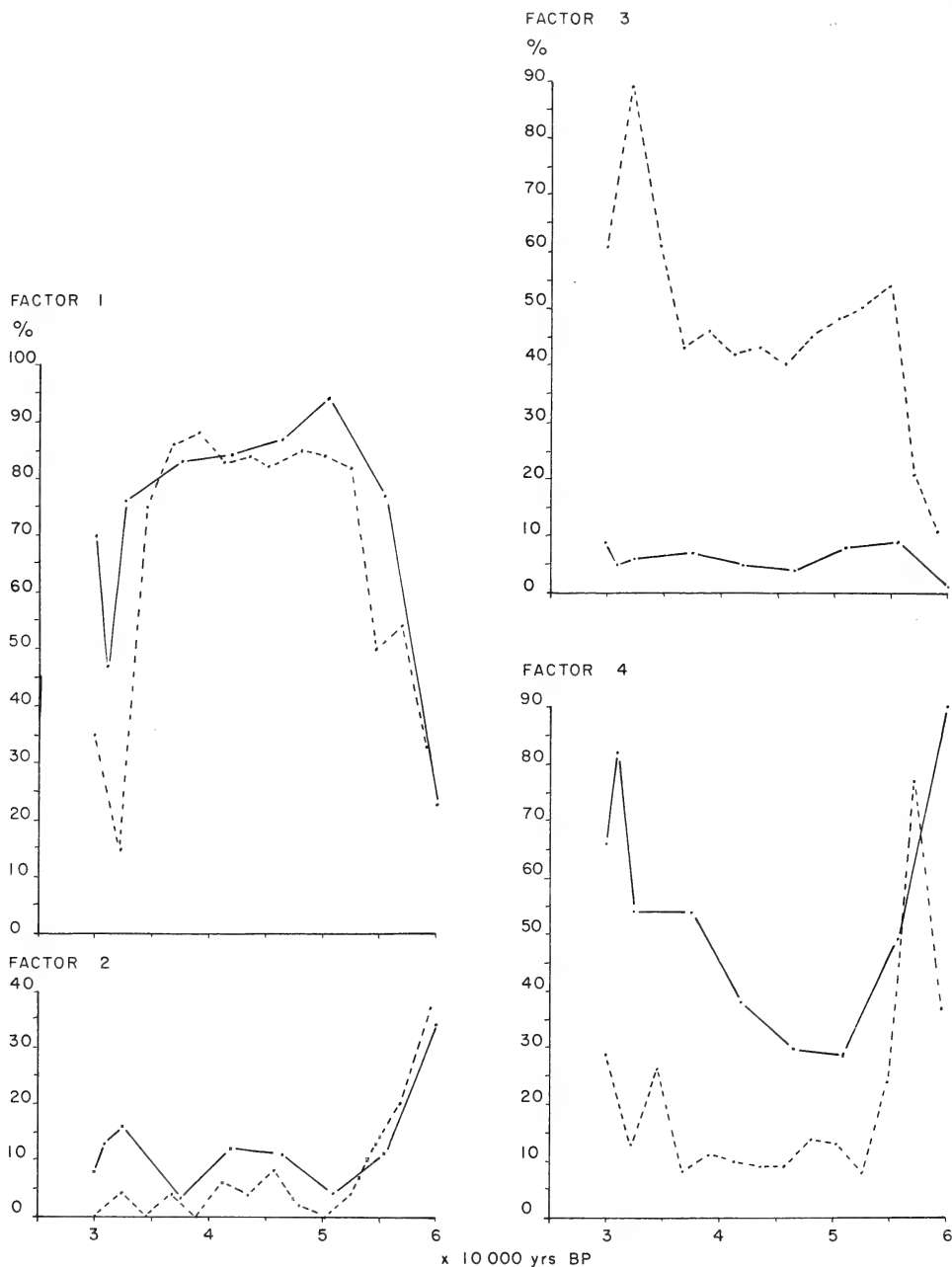


Fig. 33. Second alternative correlation of the Boomplaas A and Die Kelders 1 M.S.A. sequences. BPA levels BP3 to BOL1-3 and the DK1 M.S.A. sequence correlated using variation in percentage of total variance accounted for by factors in the Oblique rotated factor structure matrix. (Solid line = Boomplaas A; dashed line = Die Kelders 1.)

Kelders 1 M.S.A. levels were probably deposited during the same period as Boomplaas A levels BOL1 to BP3 inclusive. The approximate dates for this period are 60 000 B.P. to 30 000 B.P. The latter is based on bracketing dates of $21\,100 \pm 420$ B.P. (UW 300) for level LPC and $32\,400 \pm 700$ B.P. (UW 304) for level BP4. The former date is indicated by the fact that level BOL1 is approximately midway between level BP4 and the base of the sequence which it is suggested above is dated to about 80 000 B.P. ^{14}C determinations UW 305 and UW 308 gave readings of greater than 40 000 B.P. for levels OLP1 and BOL, while an informal date of 42 000 B.P. for level OLP1 was provided by an unnumbered Pta determination. If these dates for the Die Kelders 1 sequence prove correct, they might well not be incompatible with the bone apatite date of $31\,800^{+5000}_{-2900}$ B.P. (GX-1717) given by Schweitzer (1970) for level 5.

Establishment of the possible upper date proved more difficult than that of the lower date. Correlation of M.S.A. level 14 at Die Kelders 1 with Boomplaas A level BOL1 is good in both sets of diagrams (Figs. 32-33). On the basis of the individual species (Fig. 32) the upper limit of the correlations was first thought to lie in BPA level OLP which would have entailed a total M.S.A. period occupation of about 20 000 years for Die Kelders 1. The levels analysis (Fig. 33) indicated, however, that the best general fit was obtained by correlating BPA level BP3 with DK1 M.S.A. level 1. It was considered preferable to accept this estimate since the factor analysis had involved the whole suite of species. Moreover, such a correlation is generally consistent when applied to the individual species. It is perhaps also more reasonable that the period involved should be nearer 30 000 years in view of the fact that each level of occupation is separated from the next by possibly a considerable period of non-occupation (see Fig. 5). It has been postulated above that much of the M.S.A. occupation at Die Kelders 1 took place during the middle pleniglacial of the Last Glacial. That the levels at Boomplaas A with which it is proposed that they are correlated are similarly interpreted is seen as corroborating evidence. Moreover, this is not inconsistent with the evidence from sea-level changes reviewed by Tankard (1976*b*), which indicates an interstadial sea-level at -20 m between about 47 000 B.P. and 20 000 B.P. It is also in accord generally with the specific geological interpretation that Die Kelders 1 was first occupied during a very cold period but mostly during an interstadial (Tankard & Schweitzer 1974, 1976).

PREHISTORY AND ENVIRONMENTAL CHANGE

In this section it is proposed first to discuss current thinking on the role of the physical environment in the development of human culture. Then the archaeological and environmental evidence, as interpreted from the micro-mammalian data, is examined in an attempt to establish how the generalities may apply in the specific case of the southern Cape. Particular attention is paid to determining whether or not there is a pattern of correlation between

environmental and cultural change in the sites examined. It must be emphasized that, besides being specific, this exercise is very tentative and will require considerably greater quantities of more detailed data before anything approaching a firm generalization can be reached. Mention should also be made of the possibilities of using the palaeoenvironmental data to aid in the detailed interpretation of archaeological sequences and of showing, by an absence of environmental change, that a switch in resource utilization may be due to choice rather than necessity, and that industrial development may take place for reasons other than adaptation to environmental change. These are, however, more properly archaeological problems and, as such, will not be discussed further here.

GENERAL CONSIDERATIONS

There would appear to be general agreement that the natural (physical and biological) environment has influenced the course of human cultural development. What is not generally agreed upon is the extent and nature of that influence. It would seem most likely, however, that, on the one hand, the extent will have varied through time, being gradually reduced as men become more technologically advanced; on the other hand, the nature of the influence might well have varied according to the nature of the environment as well as to the degree of technical development. From another point of view it may perhaps be suggested that the nature of the environment could have affected man's ability to advance technologically. In any case, it could be argued that environmental change will not only act as a catalyst for cultural change but also make it easier for archaeologists to perceive the connection or relationship between the two. More particularly, in the present study, the concern is to assess the ways in which purely environmental change may be seen to have affected cultural development. Because this is primarily a study of the natural environment, only aspects of human culture possibly affected directly by environment will be considered. The complexities of culture as a whole are not relevant and, as such, are examined only generally in order to provide the context for the main discussion.

A major general controversy has centred around the extent to which the natural environment has had an overall effect on the total culture of a people (Trigger 1971). One school believes, in effect, that natural environment will determine the nature of the society's economy which, in turn, will have a major effect on the remaining aspects of that particular culture. Trigger (1971: 325) has labelled this 'determinant ecology', and it would appear that one of the main problems has been a tendency to take this idea to logical conclusions which, at best, do not fit the evidence and, at worst, are absurd. Undoubtedly the open-system ecology (Trigger 1971: 329) would seem to provide an intrinsically more realistic explanation because it emphasizes that a complex of factors must be responsible for the final result which is, after all, complex itself. It recognizes also that the human environment involves not only the natural but

also the cultural environment. This latter comprises interaction with other groups and societies, with resultant acculturation. In the present study only the natural, specifically biological, environment is to be considered, which would suggest that only part of the problem can be examined. In fact, 'open-system ecology . . . assumes that developments affecting any one aspect of culture can ultimately produce further adjustments throughout the system and affect the system's relationship with its natural environment' (Trigger 1971: 330). This is not the same as suggesting that the environment controls the culture but it does indicate that a study of the relationship between the system and the natural environment may prove more informative than may otherwise be expected.

The nature and extent of natural environmental control over the course of cultural development appear not to have been static. For example, it should be possible to assume that a group of people who subsist by hunting and gathering are more directly affected by their environment than a group of people living in a major city. Certainly climate will determine whether or not there is central heating and/or air conditioning in the buildings, but this in itself implies a level of control of the environment which allows almost total effective independence from the climate. The gradual increase in efficient acquisition of energy up to this level may be seen as basic to man's changing relationship with his environment (Klein 1979). In this process it is both the kind of energy as well as the amount that are involved. At the beginning of the process the primitive hunter-gatherers may be supposed to exist at the stage of acquiring sufficient energy from food to keep alive. Basically they will be obliged to seek food where and when it is available and at this level it is to be expected that the natural environment will exert considerable control over the activities of the people. Slight modification of the environment in the form of fire, primitive shelters and clothes may allow marginal expansion into previously uninhabitable areas, but it is likely that the availability of food will constitute the major controlling factor for hunter-gatherer societies, as Harpending & Davis (1977) have attempted to show with mathematical formulae.

Another point to be considered is that different types of environment may perhaps have different effects on cultural development. By this is meant that under harsh conditions various constraints will presumably operate that will be absent under milder conditions. Alternatively, milder conditions will provide more options than will rigorous conditions; the measure of choice of available foodstuffs, mentioned by H. J. Deacon (1972: 33), will be greater. Yellen (1977) suggests, for example, that the type of environment will affect the nature of the society living in the area. Thus, under desert conditions where food supplies are limited and unpredictable, the advantage will lie with groups that are resilient, that is, adaptable rather than specialized and without too many internal restrictions. Under milder conditions where resources are predictable and more abundant, the advantage would presumably lie with specialists. Through the archaeological record the possibility exists of examining cultural response to environmental conditions on a temporal as opposed to a spatial

basis. Thus it is possible that under adverse glacial conditions groups of resilient hunter-gatherers would have had the advantage. Their very adaptability could also, thereafter, have best fitted them to deal with changing conditions at the end of the glacial period. Under milder postglacial conditions, specialization would presumably have been an advantage. Moreover, if, as has been suggested above, the possibilities for specialization are increased under milder conditions, the archaeological record might be expected to show increased numbers of regional or local differences. If the people were unable to remain in one area throughout the year it is to be expected that they would practise a number of different specializations in different places, as was shown by Coe & Flannery (1964). Yellen (1977: 265) notes that this phenomenon has been observed in birds, which may be territorial in summer when food is abundant but not in winter when food is scarce. As far as prehistoric people are concerned, it may be that environmental change could well provide the incentive towards technical development. It must, however, be noted that the actual nature of that development would depend upon the people involved, as J. Deacon (1978: 108) has pointed out. Whether or not social behaviour could also be affected, is a more tenuous proposition.

One aspect of specialization may be the focusing of attention on smaller areas which Coe & Flannery (1964) have called microenvironments. This is not to suggest that one group of people necessarily concentrated on only one such microenvironment; indeed, they manifestly did not. Butzer (1971: 7) also makes the point that reconstruction of the immediate environment of a site is of major importance. Such reconstruction makes it possible to establish in greater detail the degree of specialization involved and, as in the case of Coe & Flannery's study (1964), the extent to which environmental differences might have encouraged or delayed improvement in subsistence strategies. They have suggested (Coe & Flannery 1964) that harsh conditions can delay progress until some method is found of artificially ameliorating those conditions, such as irrigation in an arid climate. Thus, people living under basically desert conditions were unable to make the change to full dependence on agriculture until they found a way of irrigating the crops; instead, cultivation became only one part of their annual round. On the coast, however, the milder climate allowed more and closer microenvironments which, together with agriculture, allowed the population to remain sedentary and to develop village life much earlier than the inland people. This is another aspect of the effect of environment on cultural development, which is discussed above, and it would tend to illustrate the interrelationship of all aspects.

An alternative possibility is that people will concentrate on certain plants and animals, as has been suggested by Flannery (1968). Because these resources may be found in more than one microenvironment, different groups of people may follow the same way of life in spite of living under slightly different conditions, or one group may cross-cut several microenvironments in pursuit of a particular resource. By the same token, change in the environment of one site

over a period of time need not affect the economy of the people living there, provided the relevant natural resources, plant or animal, are not affected. This is an important point which suggests that only environmental change of considerable magnitude will have forced people to change their economy. Changes of lesser magnitude may, on the other hand, have provided the means or incentive for voluntary change. It is possible that the micromammalian evidence may provide some insight into this problem. It may give an indication as to whether people were operating within or across microenvironmental boundaries and it could perhaps also, by indicating the amplitude of environmental change, suggest whether or not industrial changes were likely to have been initiated by environmental change. Flannery (1967) used the micromammalian evidence to provide background environmental data, but he did not tie this in with his interpretation of human exploitation of resources (Flannery 1968). To do this may provide some useful insight into the mechanics of subsistence.

As far as actual technological adaptation is concerned, it has been suggested that some stone industries can be correlated with particular environments. For instance, on the basis of distribution, Clark (1963: 360) has suggested that the Sangoan industry was connected with thicker vegetation and higher rainfall. He notes later regional contemporary differences in culture which he attributes to environmental differences, with a suggested correlation between smaller tools and open country and vice versa (Clark 1963: 362). This would seem to imply that the tools were used for working the vegetation in some way. Mazel & Parkington (1978) have, in fact, suggested not only that there is a correlation between high proportions of adzes and woody plants in the western Cape, but also that the adzes were used for wood-working. There is, however, still much to be done in the way of assigning uses to various stone tools, so that this purely practical aspect has yet to yield much information concerning environmental adaptation.

The open-system ecology of Trigger (1971) employs a very broad definition of environment, as was mentioned above. It was also pointed out that in the present context only a narrow definition was being considered. This implies that studies of the natural environment can be of use only in selected aspects of interpretation. For this reason it is as well to attempt to give some indication of the aspects which data from micromammalian evidence may elucidate. In general terms it may be suggested that these data will provide evidence to aid interpretation of human ecology but not, at least for the moment, of human biogeography; evidence for the relationship of people to their environment but not of their distribution in the countryside may be provided. This is because the data provide detailed information about small areas. This will enable some assessment to be made concerning adaptation to, or utilization of, local resources by the occupants of the site in question in terms of the contemporary environment. It will also enable comparison of such adaptation at different sites in different and similar environments. On the other hand, unless there is evidence from a large number of sites, it is unlikely that micromammalian

evidence will have anything to add on the subject of the distribution of human beings or their movements from one area to another. The small scale of micromammalian evidence is not appropriate to providing information concerning activities conducted on such a relatively large scale.

THE SOUTHERN CAPE PROVINCE

It is to be expected that the generalities discussed above will find specific application in the southern Cape Province. The purpose here will be to investigate the extent to which the environmental data elicited from the micromammalian evidence can be used to demonstrate a connection between cultural and environmental change. In this exercise the main advantage lies in the fact that the micromammalian evidence is closely associated with, but independent from, the archaeological evidence. The result is that the micromammalian evidence is directly relevant but avoids the risk of false correlations between human activity and environmental conditions and change. As has already been indicated, it is at the detailed local level that the importance of the micromammalian evidence will be felt. It is, therefore, at this level that the data will be examined, although reference to the known archaeological framework for the southern Cape will be made. In much of the following discussion changes in the lithic assemblages and environmental change, as interpreted from the micromammalian evidence, are compared in isolation. This has been done purely as an aid to simplifying the argument; the lithic assemblage is taken as representative of the culture to which it belongs only because it is easier to discuss changes in a concrete entity than in an abstract concept. It is not suggested either that the lithic assemblages represent the sum of archaeological reality, as discussed by Hill (1972), or that there is a deterministic relationship between technology and environment.

As a taxonomic convenience, the Upper Pleistocene and Holocene archaeological sequence of the southern Cape, and the rest of southern Africa, has been divided into two major parts, lasting respectively from about 125 000 to 40 000 B.P. and from about 40 000 B.P. onwards (Klein 1977: 120). The earlier of these is the Middle Stone Age (M.S.A.), a term originally proposed by Goodwin (Goodwin & Van Riet Lowe 1929), who described two industries and a number of variants. Subsequently, Klein (1977: 120) has remarked on the large number of different industries in the general M.S.A. category. Sampson (1974) has attempted to instil some order by grouping these into complexes. However, the mere fact that the material has been assigned to numerous industries is indicative of the variation within the material. This, together with the occurrence of sites in a wide variety of different habitats (Klein 1977: 120), could be indicative of the adaptability of the people at that time. One example is to be found at Klasies River Mouth where the people made extensive use of marine resources (Klein 1976: 83). At this and inland sites they apparently preyed upon small or larger ungulates, depending on which was more readily available, but showed a seeming reluctance to catch the fiercest animals (Klein

1977: 120). Both Klein (1976) and Sampson (1974: 256) have noted that a change in the most commonly represented antelope in the samples apparently coincided with the introduction of Howieson's Poort artefacts. It may be that both this and the earlier Stillbay—although this has yet to be properly defined (Sampson 1974: 257)—represent technological adaptations to environmental change. In general, however, it appears that there was an appreciable trend in development during approximately 100 000 years.

The apparent trend towards a cyclical effect in the M.S.A. industries may, in fact, be explained by a need to adapt to oscillating conditions. Sampson (1974: 248) remarked on the fact that the post-Howieson's Poort industries from Klasies River Mouth and Skildergat (Peer's Cave) show a marked similarity to the pre-Howieson's Poort industries. The use of prepared cores, which is a feature of the earlier cultures, is apparently absent from the later levels at Klasies River Mouth, but was found at Boomplaas A (H. J. Deacon 1977 pers. comm.). It is possible that both the earlier and the later industries may represent some form of adaptation to interglacial or interstadial conditions. If the equation of the Last Interglacial with ^{18}O stage 5e is accepted, it could be argued that M.S.A.I and perhaps M.S.A.II at Klasies River Mouth might be dated to the Last Interglacial. Klein (1976) has suggested that essentially modern conditions existed at that time, which is to be expected from what is known elsewhere for that period. Again, in the later M.S.A. there is a suggestion of conditions similar to those of the present. Klein (1978) has suggested that the evidence from the lowest levels at Boomplaas A indicates essentially modern conditions and consequently suggests a date of about 100 000 B.P. for the base of the sequence. It has been proposed above, however, that what is represented is probably an interstadial towards the end of the early last glacial and that conditions, while definitely mild, were not the same as those of the present. During the intervening period it is suggested that a colder stadial in the early glacial occurred. Klein (1977: 120) proposed that the Howieson's Poort backed blades and segments may have been hafted which, together with the increase in larger open-country bovids (Klein 1976), suggests an adaptation to different conditions during that period. Whether or not the Stillbay industry, if it exists, proves to be another such adaptation remains to be seen.

It has been observed (Klein 1974) that archaeological deposits in the southern Cape frequently exhibit a hiatus during the period when the final M.S.A. may be expected to be replaced by the early Late Stone Age (L.S.A.). One major exception has proved to be the Boomplaas A sequence (Deacon & Brooker 1976), where the interface is represented. Although the late M.S.A. material has not yet been studied in detail, its potential for providing evidence of adaptive processes is considerable. The M.S.A. is thought to have lasted until about 30 000 B.P. at Boomplaas A (H. J. Deacon 1978 pers. comm.). This is in itself an important point because it suggests that the M.S.A. people there were sufficiently resilient to cope with a considerable range of climatic

conditions, including the first maximum of the Last Glacial. At present there is no evidence to indicate that this latter event merited any major changes in the stone industry. Detailed study may, however, yet reveal such a development.

In the region of 40 000 to 30 000 B.P. the Middle Stone Age was replaced by the Late Stone Age. The evidence from Boomplaas A suggests that the transition to the first, as yet undescribed, L.S.A. industry took place before the last glacial maximum. This is an apparent anomaly but it should be noted that the micromammalian evidence indicates that conditions had been deteriorating to a certain extent for some time before that change is recognizable in the archaeological record. It may, therefore, be argued that the people had been undergoing adaptation during the same period. If this were the case, it might be merely accidental that the sum of the differences became sufficiently great to warrant the recognition of a new industry before the contemporary environmental trend had reached its climax. Perhaps an inherently more likely explanation is that, in effect, cultural change is retroactive; that is to say, the sum of the changes which are recognizable as a new industry represent the culmination of adaptation to conditions which might already have begun to change again. This might particularly be the case if the environmental changes constituted repeated reversals of trends such as are envisaged for the Upper Pleistocene. Thus in the case of Boomplaas A it may be that the early undescribed L.S.A. industry represents the results of a period of adaptation to the interpleniglacial conditions indicated by the micromammalian evidence. This may seem less likely in view of the period of climatic deterioration prior to this. On the other hand, conditions were apparently not very harsh and the period of time involved may not have been very long (see Table 44). This hypothesis would obviate the necessity of explaining why there were two different industries in the same place both adapted to glacial maximum conditions, assuming a fairly close association between industry and environment at this time.

The succeeding culture is the Robberg, which replaces the undescribed industry at Boomplaas A at the height of the last glacial maximum. If this is seen as a culmination of adaptation to environmental change, there is no anomaly in the lack of coincidence between environmental and industrial change. J. Deacon (1978: 109) has suggested that the change from one industry to another will be marked by a period of accelerated change. There would appear, however, to be no inherent reason why this need happen since, even without a postulated increase in change, it is likely that the sum of differences between industries will eventually be greater than the sum of similarities. In fact, it would appear more logical to suggest that differences in rates of change would be erratic responses to specific sets of conditions rather than part of a fixed cycle. However, there is little merit in further speculation until more information has been extracted from the material itself and it can be ascertained that all stages in the development of the industry are represented in a particular site. If such evidence is found, it is likely that detailed micromamma-

lian evidence for the contemporary environment would provide considerable insight into the incentives for, and delays in, effecting industrial change.

According to the argument put forward above, under changing conditions an industry could be expected to show its purest form and best adaptation to prevailing conditions in its early stages. Subsequently, because the industry might be supposed to become increasingly ill-adapted, changes would be instituted that would ultimately require definition of another industry. It must, incidentally, be pointed out at this stage that only high-level between-industry change is being examined; low-level so-called stylistic change within one industry is thought to represent response to quite different stimuli, perhaps social or aesthetic (J. Deacon 1978). Although generalizations are inadvisable, the evidence for the Robberg industry suggests that this scheme may have some wider application beyond the Boomplaas A sequence. It has previously been suggested that the Robberg industry represents an adaptation to glacial conditions (Klein 1972a, 1978; J. Deacon 1978), which agrees with the suggestion made above. It is to be noted, however, that at Boomplaas A the Robberg is also temporally correlated with the late glacial, which was apparently a period of considerable amelioration of conditions. It is logical to suggest, therefore, that the Robberg must have become increasingly ill-adapted as conditions changed. The evidence from Nelson Bay Cave is instructive in this respect. Here the micromammalian evidence confirms that at least the earlier part of the Robberg industry relates to glacial conditions. Unfortunately, there is no micromammalian evidence for the later levels. However, the fact that J. Deacon (1978) points out that the sample from level BSL, which she has placed with the Robberg, is actually intermediate between the Robberg and the succeeding Albany, is surely indicative of a situation similar to that postulated for Boomplaas A.

The next major industrial change is recognized at about 12 000 B.P. in the southern Cape at Nelson Bay Cave (J. Deacon 1978) and at Boomplaas A (H. J. Deacon 1979). There is also a possibility of an industrial change at Byneskranskop 1 at a similar time (Klein 1981) although Schweitzer & Wilson (1978) point out that the paucity of remains in the lower levels makes comparison difficult. At the first two sites, however, the industry has been identified as Albany (J. Deacon 1978; Deacon *et al.* 1976). This industry is seen as an adaptation to changing conditions and, as such, it is expected that it should exhibit either a number of distinct sub-phases or a generality which would ensure its suitability to a variety of conditions. This latter may be suggested by the fact that at Nelson Bay Cave the Albany samples contain a smaller variety of formal tools than do the Wilton or Robberg samples (J. Deacon 1978: 94). It may, however, prove easier to establish the fine mechanics of adaptation at Boomplaas A where the excavation of fine stratigraphic units should allow analysis of discrete phases if such exist. It is interesting to note here that at Boomplaas A the micromammalian evidence indicates fluctuations, albeit of lesser amplitude, during the early Holocene at the time when the Albany

industry was being employed. This may suggest a reason for the continued usefulness of the industry after the beginning of the Holocene. It is also possible that the unnamed pre-Wilton industry at Byneskranskop 1 will prove to be a similar adaptation to somewhat fluctuating conditions. Since, however, there is some possibility that conditions were changing more rapidly in the Congo valley than at Byneskranskop 1 during this period, it may be that this would have some effect on industrial development in the two areas. It may, of course, prove impossible to separate the putative effects of this factor from those of others, but it is still worth bearing in mind that it may exist.

The establishment of essentially modern, basically stable conditions in the southern Cape may probably be correlated with the appearance of the Wilton industry. It is suggested that the improved conditions will have provided a greater range of possibilities from which the people might choose their *modus vivendi*. At the same time it could be postulated that greater reliability of resources would encourage specialization. H. J. Deacon (1972: 27) has criticized Clark's (1959: 189) characterization of the Wilton as a 'period of regional specialization par excellence' as having 'no basis in the understanding of the effective environment in which the culture systems operated'. It may, however, be that the fault lies not in the concept but in the level of generalization. If specialization is to be assessed, it should perhaps be examined at the level of individual microenvironments rather than on a regional level. At the more specific level there is much to recommend the hypothesis that the Wilton culture involved considerable specialization. This process should probably be seen in terms of multiple specialization by each group of people. The increasing evidence for seasonal migration (H. J. Deacon 1969; Parkington 1972, 1976) would suggest that this must have been the case. Klein (1974a: 275) has noted that the coastal Wilton people exhibited an increasing tendency to exploit marine resources and G. Avery (1974, 1976) has recorded concentration on different species of shellfish by Pottery Wilton people. Inland there is evidence for the exploitation of both selected plant foods and freshwater shellfish (H. J. Deacon 1972). H. J. Deacon (1972: 34) also suggested that a low proportion of segments and backed blades in the eastern Cape assemblages relative to those from Zambia may indicate the use of traps to catch small bovids in the former area, whereas projectile points were used to hunt larger bovids in the latter area. Finally, H. J. Deacon (1972: 39) sums up the situation as an 'apparent trend towards an increasingly wider range of resources on an increasingly intensive scale'.

The micromammalian evidence has nothing to add on any possible correlation between culture and environment. There is insufficient evidence to allow any spatial correlations because, as has already been mentioned, a large number of observations would be necessary before this could be attempted. However, such evidence as there is from Boomplaas A and Byneskranskop 1 provides some indication of the local environment of the site which could be useful for checking possible specializations at each site. Changes within the

Holocene are hardly monitored by the micromammalian evidence and it is suggested that changes must have been relatively minor. It will consequently be necessary to acquire a more sensitive indicator for this period before it is possible to determine whether or not there is any connection between environmental change and industrial development. It is possible on logical grounds to argue that the low-level changes witnessed in the Wilton (J. Deacon 1972) may, in fact, represent adaptations to low-level environmental changes. It would be interesting to find a means of assessing the more likely truth of the matter.

It is of considerable importance to point out, with H. J. Deacon (1972: 39), that resource utilization cannot be seen simply as a response to environmental conditions, or industrial development as direct cause and effect (J. Deacon 1978: 108). While it is most unlikely that this was the case at any time, there is ample evidence from the Holocene for management of natural resources and the environment. Evidence for the building of shelters and the use of fire, the storage of food first in pits and then, presumably, in pots, and the later introduction of sheep herding all point towards a greater independence from environmental variables which, in turn, allows greater freedom of choice in any given situation. It does, however, appear that the coincidence of a naturally induced increase in options and an improved human technical skill could have provided useful impetus for major cultural changes. That these changes involved more than economic adaptation is suggested by the first appearance of items of personal adornment and burials (Klein 1977) in Wilton contexts, which presumably represent some sort of change in attitude towards the individual and the group. Similarly, both Klein (1977) and H. J. Deacon (1972) remark upon the evidence for changes in social structure and demography during the later Holocene. All these aspects speak for the increasing cultural complexity and, if one may so phrase it, civilization of the people responsible.

The available evidence suggests that, in so far as the lithic industry may be taken as representative of a total culture, there may be some reason to suppose that a correlation does exist between cultural and environmental change. This is particularly the case with industries prior to the Wilton, which would be in accordance with the suggestion that less technically advanced hunter-gatherer societies will be closely dependent upon their environment. The evidence goes on to indicate that the Wilton people displayed an increasing independence from natural vicissitudes which may be expected to have as a corollary a development increasingly independent of any direct environmental stimulus. The converse is that later human activities almost certainly began to have a significant effect upon the environment. The introduction of sheep herding to the southern Cape at the end of the period under discussion in the study (Schweitzer & Scott 1973; Deacon *et al.* 1978) must certainly have formed a major step in this process, but it may well have begun before that time. For instance, H. J. Deacon (1976: 174) has postulated that people may have deliberately fired the vegetation to promote the growth of *Watsonia* sp., the corms of which constituted an important source of food (H. J. Deacon 1976:

162). This would undoubtedly have affected the vegetation, even if not to the extent subsequently resulting from firing to improve grazing for domestic stock. Klein (1972*b*) has suggested that improved hunting techniques may ultimately have been responsible for the extinction of some bovid species at the end of the Last Glacial. Although none of the evidence is adequate to prove any hypothesis concerning the role of environment in cultural development, the data discussed do suggest that the micromammalian evidence will prove useful to any further work in this direction.

CONCLUSIONS

It was stated in the introduction that the principal aim of the present study was to provide detailed information concerning the natural environment in which past people existed. There is already considerable evidence to show that micromammalian remains can be used to provide such information; it was not, therefore, necessary to prove this point. There are, however, a number of ways in which the basic material may be approached in order to extract environmental information and it was considered important to determine the potential of each and the precise nature of the evidence provided. It was necessary, as a preliminary stage in the interpretation of the data, to establish both the approximate relationship of the available sample to the living community from which it was derived and also the ecological significance of individual species. Since micromammalian data provide one of several lines of evidence for environmental change, this line must be fitted into, and checked against, the general known scheme. This is particularly important because this evidence is very local in application and does not necessarily come from uninterrupted sequences.

There are considerable advantages to using micromammalian evidence for the interpretation of the environment of prehistoric people. Not only is the evidence contemporary but it also refers unquestionably to the neighbourhood of the site from which the sample came. The evidence is, moreover, independent of the archaeological evidence, which is extremely important, and it is also capable of providing very detailed information concerning the environment at a given time. Further, it has the potential, given the right controls, for indicating both rates and amplitudes of environmental change through time. Finally, the time lag in response to environmental change is almost certainly minimized by the small size and consequent relative sensitivity and rapid breeding of micromammals.

As far as the material itself is concerned, the initial good sample collected by *Tyto alba* (barn owl) is thought not to suffer much differential destruction because the specimens are of a similar size, and the fact that only the jaws were counted provided each individual with an equal chance of being represented in the sample. The relatively frequent occurrence of large samples greatly extends the range of possible studies that may be conducted and allows reliable statistical analyses to be performed.

Disadvantages relate to the small size both of the area represented by the evidence and of the animals themselves. In the first place the situation can be rectified by the acquisition of greater numbers of samples. In the second case the fact that the material may easily be broken or overlooked can affect the completeness of the sample, but such biases can be reduced if great care is taken in the collection of samples. Although large samples will allow studies of population and community structure, they contain a degree of heterogeneity, the elements of which it will not normally be possible to isolate. The level of detail in interpretation will, therefore, be reduced, but this is an unavoidable feature of fossil assemblages.

Of the three main lines of approach, one has been shown to relate principally to vegetation changes and the others to climatic changes. The former concerns changes in the composition of the community. Although it is suggested that the immediate reason for changes in the proportions of some species may be response to changes in other species, the ultimate cause of changes is thought to have been shifts in the vegetational mosaic of the area in question. Fluctuations in temperature and probably rainfall are reflected in changes in the mean size of the individual in different populations. If the means for different populations are compared, it is quite clear that some species exhibit considerable variation in size both geographically and temporally. At the community level there are also marked differences in structure which are interpreted as reflecting changes in general climatic conditions at various times in the past.

It is clear that there is considerable detail to be extracted from these various lines of approach and the ultimate goal would seem to be a degree of quantification of the data. At the present, however, there does not exist the basic information relating to living representatives of the species involved. When the data become available it should be possible to determine much more precisely the vegetational shifts represented by the observed changes in composition of the small-mammal communities. As an aid to this, increased knowledge of interspecific behaviour should allow a better chance of isolating the various mechanisms of change in community structure. Easier to collect will probably be data concerning correlation of size variation and climatic factors. Here again, though, it may be difficult to establish a direct link between, for example, temperature and size, and even range and variability of temperature could have different effects. There is, however, no doubt that considerable advances must become possible once more detailed knowledge is gained of existing small-mammal species.

Although the particular purpose of the present study was to furnish an aid to the interpretation of human prehistory, it must be noted that the study of micromammalian remains has considerable intrinsic interest. Apart from the fact that the provision of evidence for palaeoenvironmental fluctuations and conditions is important in its own right, the material also contains good potential for the study of small mammals themselves. Just as information from

modern representatives can aid interpretation of past data, so subfossil material can provide insight into the biogeography, palaeoecology and general development of extant species.

SUMMARY

Facts concerning the topography, climate and vegetation of the southern Cape Province were given briefly as a background to the more detailed descriptions of the individual sites which yielded micromammalian samples. The material itself was discussed both in practical terms, from the point of view of its collection and identification, and in more theoretical terms. These latter concern not only how the material entered the cave, but also what biases may have resulted from this method and subsequent taphonomic processes. Biases inherent in micromammalian evidence were also discussed, the aim in general being to establish what relationship any interpretation may bear to reality. The basis which small mammals provide for interpretation was then examined. This involved ascertaining as accurately as possible the habitat requirements of individual species, after which each species was taken as representative of those conditions. Control data from modern accumulations were then checked against the known existing situation.

Existing evidence for palaeoenvironmental change is available from marine and terrestrial geology and from the analysis of pollen and remains of animals other than small mammals. These data were synthesized as a preliminary to checking the interpretation from the small mammals and in order to provide a framework into which the latter could be fitted. The micromammalian data themselves were examined mainly from the point of view of community composition. Changes in this provided good evidence of vegetational change during the period under review. Changes in community structure, measured with various indices of diversity, gave some indication of general relative climatic conditions at different times. Changes in the mean size of the individual in various populations of selected species also suggested that there was climatic change during the last 80 000 years. An overall reconstruction was based on all these aspects and provided a picture which could be readily correlated with other lines of evidence and appeared to be generally accurate as well as more specific and detailed than most evidence.

The possibility exists of using the pattern of environmental change thus acquired to correlate archaeological sequences which are undated or insecurely dated. If the patterns of change at two sites can be matched, the likelihood exists that they represent the same period of time, subject, of course, to gross temporal controls.

The application of the evidence acquired from micromammals to archaeology could be fairly wide. Knowledge is gained of conditions in the immediate vicinity of the occupation site. It was shown that, given sufficient material, it is possible to provide detailed evidence of change which is tied securely to the

archaeological sequence but from which it is independent. It was postulated that this could make it feasible to establish whether there exists any correlation between environmental change and alterations in prehistoric technology and economy.

ACKNOWLEDGEMENTS

The present study, which is an amended version of a thesis accepted for the degree of Doctor of Philosophy at the University of Stellenbosch, resulted directly from the advice and encouragement of Prof. R. G. Klein, University of Chicago. The constructive criticism of Prof. H. J. Deacon, University of Stellenbosch, and of Prof. Klein during their supervision of the research is appreciated. Prof. Klein also generously made available various unpublished data. Mr G. Avery is thanked sincerely for his help in all aspects of the work. Thanks also go to Prof. Deacon for making available the Boomplaas A sample, and to Mr F. R. Schweitzer and Dr Q. B. Hendey for allowing access to the remaining samples which are lodged in the South African Museum. Modern samples were collected by Miss K. Scott and Mr Avery; Mr T. N. Pocock kindly provided a checklist of the Windheuveld material examined by him. Mr T. P. Volman, University of Chicago, and Dr N. J. le Roux, University of Stellenbosch, were of great help with the factor analysis but cannot be held responsible for any errors. Thanks are also due to Dr G. de Graaff, National Parks Board, for generously offering access to his unpublished manuscript, and to those who kindly answered requests for information; individual items are acknowledged as personal communications in the text. The typing of much of the manuscript by Mrs M. Scheiner and Mrs P. Wallendorf is greatly appreciated.

REFERENCES

- ACOCKS, J. P. H. 1975. Veld types of South Africa. *Mem. bot. Surv. S. Afr.* **40**: 1-128.
- ANDREWS, P., GROVES, C. P. & HORNE, J. F. M. 1975. Ecology of the lower Tana River flood plain (Kenya). *J. E. Afr. nat. Hist. Soc. & natl Mus.* **151**: 1-31.
- ANSELL, W. F. H. 1960. *Mammals of Northern Rhodesia*. Lusaka: Government Printer.
- ANSELL, W. F. H. & ANSELL, P. D. H. 1973. Mammals of the north-eastern montane areas of Zambia. *Puku* **7**: 21-69.
- AVERY, D. M. 1977. Past and present distribution of some rodent and insectivore species in the southern Cape Province, South Africa: new information. *Ann. S. Afr. Mus.* **74**: 201-209.
- AVERY, G. 1974. Open station shell midden sites and associated features from the Pearly Beach area, south-western Cape. *S. Afr. archaeol. Bull.* **29**: 104-114.
- AVERY, G. 1976. A systematic investigation of open station shell midden sites along the south-western Cape coast. Unpublished M.A. thesis, University of Cape Town.
- BADA, J. L. & DEEMS, L. 1975. Accuracy of dates beyond the ^{14}C dating limit using the aspartic acid racemization technique. *Nature, Lond.* **255**: 218-219.
- BE, A. W. H. & DUPLESSY, J. C. 1976. Subtropical convergence fluctuations and Quaternary climates in the middle latitudes of the Indian Ocean. *Science* **194**: 419-421.
- BEHRENSMEYER, A. K. 1975. The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bull. Mus. comp. Zool.* **146**: 473-578.

- BIGALKE, R. C. 1978. Mammals. In: WERGER, M. J. A., ed. *Biogeography and ecology of southern Africa. Monogr. biol.* **31**: 981-1048.
- BINFORD, L. R. & BERTRAM, J. B. 1977. Bone frequencies—and attritional processes. In: BINFORD, L. R. ed. *For theory building in archaeology*: 77-153. New York: Academic Press.
- BODENHEIMER, F. S. 1949. *Problems of vole populations in the Middle East. Report on the population dynamics of the Levant vole (Microtus guentheri D. et A.)*. Jerusalem: Research Council of Israel.
- BOND, W., FERGUSON, M. & FORSYTH, G. 1980. Small mammals and habitat structure along altitudinal gradients in the southern Cape mountains. *S. Afr. J. Zool.* **15**: 34-43.
- BRAIN, C. K. 1967. Hottentot food remains and their bearing on the interpretation of fossil bone assemblages. *Sci. Pap. Namib Des. Res. Sta.* **32**: 1-11.
- BRAIN, C. K. 1969. New evidence for climatic change during Middle and Late Stone Age times in Rhodesia. *S. Afr. archaeol. Bull.* **24**: 127-143.
- BRAIN, C. K. 1974. The use of microfaunal remains as habitat indicators in the Namib. *S. Afr. archaeol. Soc. Goodwin Ser.* **2**: 55-60.
- BRAIN, C. K. & BRAIN, V. 1977. Microfaunal remains from Mirabib: some evidence of palaeoecological changes in the Namib. *Madoqua* **10**: 285-293.
- BRAIN, C. K. & MEESTER, J. 1964. Past climatic changes as biological isolating mechanisms in southern Africa. In: DAVIS, D. H. S., ed. *Ecological studies in southern Africa*: 332-340. The Hague: W. Junk.
- BROOKS, P. M. 1974. The ecology of the four-striped field mouse, *Rhabdomys pumilio* (Sparman, 1784), with particular reference to a population on the Van Riebeeck Nature Reserve, Pretoria. Unpublished D.Sc. thesis, University of Pretoria.
- BUTZER, K. W. 1971. *Environmental archaeology*. 2nd ed. London: Methuen.
- BUTZER, K. W. 1973. Geology of Nelson Bay Cave, Robberg, South Africa. *S. Afr. archaeol. Bull.* **28**: 97-110.
- BUTZER, K. W. 1974. Reflections on the stability of Holocene environmental zonation in South Africa. *S. Afr. archaeol. Soc. Goodwin Ser.* **2**: 37-38.
- BUTZER, K. W. 1978. Sediment stratigraphy of the Middle Stone Age sequence at Klasies River Mouth, Tzitzikamma coast, South Africa. *S. Afr. archaeol. Bull.* **33**: 141-151.
- BUTZER, K. W. & HELGREN, D. M. 1972. Late Cenozoic evolution of the Cape coast between Knysna and Cape St Francis, South Africa. *Quat. Res.* **2**: 143-169.
- BUTZER, K. W., FOCK, G. J., STUCKENRATH, R. & ZILCH, A. 1973. Palaeohydrology of late Pleistocene lake, Alexandersfontein, Kimberley, South Africa. *Nature, Lond.* **243**: 328-330.
- BUTZER, K. W., STUCKENRATH, R., BRUZEWICZ, A. J. & HELGREN, D. M. 1978. Late Cenozoic paleoclimates of the Gaap Escarpment, Kalahari margin, South Africa. *Quat. Res.* **10**: 310-339.
- CARTMILL, M. 1967. The Early Pleistocene mammalian microfaunas of sub-Saharan Africa and their ecological significance. *Quaternaria* **9**: 169-197.
- CATTELL, R. F. 1965a. Factor analysis: an introduction to essentials (I) the purpose and underlying models. *Biometrics* **21**: 190-215.
- CATTELL, R. F. 1965b. Factor analysis: an introduction to essentials (II) the role of factor analysis in research. *Biometrics* **21**: 405-435.
- CHALINE, J. 1972. *Les rongeurs du Pléistocène moyen et supérieur de France*. Cahiers de Paléontologie. Paris: Editions du C.N.R.S.
- CHITTY, D. 1960. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* **38**: 99-113.
- CLARK, J., BEERBOWER, J. R. & KIERTZKE, K. K. 1967. Oligocene sedimentation, stratigraphy, paleoecology and paleoclimatology in the Big Badlands of South Dakota. *Fieldiana: geol. Mem.* **5**: 1-158.
- CLARK, J. D. 1959. *The prehistory of southern Africa*. Harmondsworth: Penguin.
- CLARK, J. D. 1963. Ecology and culture in the African Pleistocene. *S. Afr. J. Sci.* **59**: 353-366.
- CLASON, A. T. 1972. Some remarks on the use and interpretation of archaeozoological data. *Helinium* **12**: 139-153.
- COE, M. D. & FLANNERY, K. V. 1964. Microenvironments and Mesoamerican prehistory. *Science* **143**: 650-654.

- COETZEE, C. G. 1963. The prey of owls in the Kruger National Park as indicated by owl pellets collected during 1960–61. *Koedoe* **6**: 115–125.
- COETZEE, C. G. 1969. The distribution of mammals in the Namib desert and adjoining inland escarpment. *Scient. Pap. Namib Des. Res. Sta.* **40**: 23–36.
- COETZEE, C. G. 1971. Genus *Steatomys*. In: MEESTER, J. & SETZER, H. W., eds. *The mammals of Africa: an identification manual*. Washington: Smithsonian Institution Press.
- COETZEE, C. G. 1972. The identification of southern African small mammal remains in owl pellets. *Cimbebasia* (A) **2**: 53–64.
- COETZEE, C. G. 1975. The biology, behaviour and ecology of *Mastomys natalensis* in southern Africa. *Bull. Wld Hlth Org.* **52**: 637–644.
- COETZEE, J. A. 1967. Pollen analytical studies in East and southern Africa. *Palaeoecol. Afr.* **3**: 1–146.
- COON, C. S. 1962. *The origin of races*. London: Jonathan Cape.
- CORBET, G. B. & HANKS, J. 1968. A revision of the elephant-shrews, family Macroscelididae. *Bull. Br. Mus. nat. Hist. (Zool.)* **16**: 47–111.
- COWGILL, G. L. 1968. Archaeological applications of factor, cluster and proximity analysis. *Amer. Antiquity* **33**: 367–375.
- CRAIGHEAD, J. J. & CRAIGHEAD, F. C. 1956. *Hawks, owls and wildlife*. Harrisburg: Stackpole.
- DANSGAARD, W., JOHNSEN, S. J., CLAUSEN, H. B. & LANGWAY, C. C. 1971. Climatic record revealed by the Camp Century ice core. In: TUREKIAN, K. K. ed. *The late Cenozoic glacial ages*: 37–56. New Haven: Yale University Press.
- DAVIES, O. 1971. Pleistocene shorelines in the southern and south-eastern Cape Province (Part 1). *Ann. Natal Mus.* **21**: 183–223.
- DAVIES, O. 1972. Pleistocene shorelines in the southern and south-eastern Cape Province (Part 2). *Ann. Natal Mus.* **21**: 225–279.
- DAVIS, D. H. S. 1958. Notes on small mammals in the Kalahari Gemsbok National Park, with special reference to those preyed upon by barn owls. *Koedoe* **1**: 184–188.
- DAVIS, D. H. S. 1959. The barn owl's contribution to ecology and palaeoecology. *Proc. 1st Pan-Afr. Ornith. Congr. Ostrich suppl.* **3**: 144–153.
- DAVIS, D. H. S. 1962. Distribution patterns of southern African Muridae, with notes on some of their fossil antecedents. *Ann. Cape prov. Mus.* **2**: 56–76.
- DAVIS, D. H. S. 1965. Classification problems of African Muridae. *Zool. afr.* **1**: 121–145.
- DAVIS, D. H. S. 1966. The small rodents of the Transvaal: some taxonomic, biogeographic, economic and health problems. *Fauna Flora, Pretoria* **17**: 4–12.
- DAVIS, D. H. S. 1974. The distribution of some small southern African mammals (Mammalia: Insectivora, Rodentia). *Ann. Transv. Mus.* **29**: 135–184.
- DAVIS, R. M. 1973. The ecology and life history of the vlei rat, *Otomys irroratus* (Brants, 1827), on the Van Riebeeck Nature Reserve, Pretoria. Unpublished D.Sc. thesis, University of Pretoria.
- DEACON, H. J. 1969. Melkhoutboom Cave, Alexandria District, Cape Province: a report on the 1967 excavation. *Ann. Cape prov. Mus. (nat. Hist.)* **6**: 141–169.
- DEACON, H. J. 1972. A review of the post-Pleistocene in South Africa. *S. Afr. archaeol. Soc. Goodwin Ser.* **1**: 26–45.
- DEACON, H. J. 1976. Where hunters gathered. *S. Afr. archaeol. Soc. monogr. Ser.* **1**: 1–232.
- DEACON, H. J. 1979. Excavations at Boomplaas Cave—a sequence through the Upper Pleistocene and Holocene in South Africa. *Wld Archaeol.* **10**: 241–257.
- DEACON, H. J. & BROOKER, M. 1976. The Holocene and Upper Pleistocene sequence in the southern Cape. In: *Proc. sth Afr. Soc. Quat. Res., Ann. S. Afr. Mus.* **71**: 203–214.
- DEACON, H. J., DEACON, J. & BROOKER, M. 1976. Four painted stones from Boomplaas Cave, Oudtshoorn District. *S. Afr. archaeol. Bull.* **31**: 141–145.
- DEACON, H. J., DEACON, J., BROOKER, M. & WILSON, M. L. 1978. The evidence for herding at Boomplaas Cave in the southern Cape, South Africa. *S. Afr. archaeol. Bull.* **33**: 39–65.
- DEACON, J. 1972. Wilton: an assessment after fifty years. *S. Afr. archaeol. Bull.* **27**: 10–48.
- DEACON, J. 1978. Changing patterns in the late Pleistocene/early Holocene prehistory of southern Africa as seen from the Nelson Bay Cave stone artifact sequence. *Quat. Res.* **10**: 84–111.
- DEAN, W. R. J. 1973. Age distribution of *Praomys natalensis* in *Tyto alba* pellets. *Zool. afr.* **8**: 140.

- DEAN, W. R. J. 1977. The ecology of owls at Barberspan, Transvaal. *Proc. Symp. Afr. predatory Birds*: 25-45.
- DE GRAAFF, G. 1960. A preliminary investigation of the mammalian microfauna in Pleistocene deposits of caves in the Transvaal System. *Palaeont. afr.* 7: 59-118.
- DE GRAAFF, G. 1974. Notes on the occurrence of rodents in South African national parks. *Koedoe* 17: 173-183.
- DE GRAAFF, G. 1981. *The rodents of South Africa*. Durban: Butterworth.
- DE GRAAFF, G. & NEL, J. A. J. 1970. Notes on the smaller mammals of the eastern Cape national parks. *Koedoe* 13: 147-149.
- DELANEY, M. J. 1972. The ecology of small rodents in tropical Africa. *Mamm. Rev.* 2: 1-42.
- DELANEY, M. J. & NEAL, B. R. 1966. A revue of the Muridae (Order Rodentia) of Uganda. *Bull. Br. Mus. nat. Hist. (Zool.)* 13: 295-355.
- DE MENESES CABRAL, J. C. 1966. Some new data on Angolan Muridae. *Zool. afr.* 2: 193-203.
- DINGLE, R. V. & ROGERS, J. 1972. Pleistocene palaeogeography of the Agulhas Bank *Trans. R. Soc. S. Afr.* 40: 155-165.
- DORAN, J. E. & HODSON, F. R. 1975. *Mathematics and computers in archaeology*. Edinburgh: Edinburgh University Press.
- DORST, J. & DANDELLOT, P. 1970. *A field guide to the larger mammals of Africa*. London: Collins.
- EMILIANI, C. 1955. Pleistocene temperatures. *J. Geol.* 63: 538-578.
- EMILIANI, C. 1966. Paleotemperature analysis of Caribbean cores P6304-8, P6304-9 and a generalised temperature curve for the last 425 000 years. *J. Geol.* 74: 109-126.
- EMILIANI, C. 1972. Quaternary paleotemperatures and the duration of high-temperature intervals. *Science* 178: 398-401.
- ESTES, R. D. 1971. Social organisation of the African Bovidae. In: GEIST, V. & WALTHER, F., eds. *The behaviour of ungulates and its relation to management*. IUCN Publs 24: 166-205.
- EWER, R. F. 1967. The fossil hyaenids of Africa—a reappraisal. In: BISHOP, W. W. & CLARK, J. D., eds. *Background to evolution in Africa*: 109-123. Chicago: University of Chicago Press.
- FAGAN, B. M. 1960. The Glentyre shelter and Oakhurst re-examined. *S. Afr. archaeol. Bull.* 15: 80-94.
- FAIRBRIDGE, R. W. 1961. Eustatic changes in sea-level. In: AHRENS, L. H., PRESS, F., RANKAMA, K. & RUNCORN, S. K., eds. *Physics and chemistry of the earth* 4: 99-185. London: Pergamon Press.
- FAIRBRIDGE, R. W. 1971. Quaternary shoreline problems at INQUA 1969. *Quaternaria* 15: 1-17.
- FERRAR, A. A. & WALKER, B. H. 1974. An analysis of herbivore/habitat relationships in Kyle National Park, Rhodesia. *J. sth Afr. Wildl. Mgmt Ass.* 4: 137-147.
- FLANNERY, K. V. 1967. Vertebrate fauna and hunting patterns. In: BYERS, D. S. ed. *The prehistory of the Tehuacan Valley. I. Environment and subsistence*: 132-177. Austin & London: University of Texas Press.
- FLANNERY, K. V. 1968. Archeological systems theory and early Mesoamerica. In: MEGGARS, B. J., ed. *Anthropological archeology in the Americas*: 67-88. Washington: Anthropological Society of Washington.
- FLINT, R. F. 1976. Physical evidence of Quaternary climatic change. *Quat. Res.* 6: 519-528.
- GLUE, D. E. 1967. Prey taken by the barn owl in England and Wales. *Bird Study* 14: 169-183.
- GOODWIN, A. J. H. & VAN RIET LOWE, C. 1929. The Stone Age cultures of South Africa. *Ann. S. Afr. Mus.* 27: 1-289.
- GRAYSON, D. K. 1978. Minimum numbers and sample size in vertebrate faunal analysis. *Amer. Antiquity* 43: 53-65.
- GRINDLEY, J., SIEGFRIED, W. R. & VERNON, C. J. 1973. Diet of the barn owl in the Cape Province. *Ostrich* 44: 266-267.
- GUILCHER, A. 1969. Pleistocene and Holocene sea level changes. *Earth-Sci. Rev.* 5: 69-97.
- GUILDAY, J. E. 1971. The Pleistocene history of the Appalachian mammal fauna. In: HOLT, P. C., ed. *The distributional history of the biota of the southern Appalachians. III. Vertebrates*. Virginia Polytech. Inst. State Univ. Res. Div. Monogr. 4: 233-262.
- HANNEY, P. 1962. An aid to the identification of skulls of some small Nyasaland mammals. *Rep. Bull. Nyasaland Mus.* 1962: 34-38.

- HANNEY, P. 1963. Observations upon the food of the barn owl (*Tyto alba*) in southern Nyasaland, with a method of ascertaining population dynamics of rodent prey. *Ann. Mag. nat. Hist.* (13) **6**: 305–313.
- HANNEY, P. 1965. The Muridae of Malawi (Africa: Nyasaland). *J. Zool.* **146**: 577–633.
- HARPENDING, H. & DAVIS, H. 1977. Some implications for hunter–gatherer ecology derived from the spatial structure of resources. *Wld Archaeol.* **8**: 275–286.
- HAYS, J. D., LOZANO, J. A., SHACKLETON, N. J. & IRVING, G. 1976. Reconstruction of the Atlantic and western Indian Ocean sectors of the 18 000 B.P. Antarctic Ocean. In: CLINE, R. M. & HAYS, J. D., eds. *Investigation of late Quaternary paleoceanography and paleoclimatology*. *Geol. Soc. Amer. Mem.* **145**: 337–372.
- HENDEY, Q. B. 1974. The late Cenozoic Carnivora of the south-western Cape Province. *Ann. S. Afr. Mus.* **63**: 1–369.
- HIGHAM, C. F. W. 1967. Faunal sampling and economic prehistory. *Z. Säugetierk.* **33**: 297–305.
- HILL, J. N. 1972. The methodological debate in contemporary archaeology: a model. In: CLARK, D. L., ed. *Models in archaeology*: 61–107. London: Methuen.
- HIRST, S. M. 1975. Ungulate–habitat relationships in a South African woodland/savanna ecosystem. *Wildl. Monogr.* **44**: 1–60.
- HOFMANN, R. R. & STEWART, D. R. M. 1972. Grazer or browser: a classification based on the stomach-structure and feeding habits of East African ruminants. *Mammalia* **36**: 226–240.
- HONER, M. R. 1963. Observations on the barn owl (*Tyto alba guttata*) in the Netherlands in relation to its ecology and population fluctuations. *Ardea* **51**: 158–195.
- HUBBARD, C. A. 1972. Observations on the life histories and behaviour of some small rodents from Tanzania. *Zool. afr.* **7**: 419–449.
- HUFFAKER, C. B. & MESSENGER, P. S. 1964. The concept and significance of natural control. In: DEBACH, P., ed. *Biological control of insects and weeds*: 74–117. London: Chapman & Hall.
- IMBRIE, J. & KIPP, N. G. 1971. A new micropaleontological method for quantitative paleoclimatology: application to a late Pleistocene Caribbean core. In: TUREKIAN, K. K., ed. *The late Cenozoic glacial ages*: 71–183. New Haven: Yale University Press.
- IMBRIE, J., VAN DONCK, J. & KIPP, N. G. 1973. Paleoclimatic investigation of a late Pleistocene Caribbean deep-sea core: comparison of isotopic and faunal methods. *Quat. Res.* **3**: 10–38.
- JARMAN, P. J. 1974. The social organisation of antelope in relation to their ecology. *Behaviour* **48**: 215–267.
- JARVIS, J. U. M. & DAVID, J. n.d. Population ecology of the striped field mouse *Rhabdomys pumilio* on the Cape Flats, including their dependence on invasive Acacias. In: *Fynbos research project: first annual research meeting (unedited abstracts)*. (Duplicated.)
- JOHNSON, S. J., DANSGAARD, W., CLAUSEN, H. B. & LANGWAY, C. C. 1972. Oxygen isotope profiles through the Antarctic and Greenland ice sheets. *Nature, Lond.* **235**: 429–434.
- KIM, J. 1975. Factor analysis. In: NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. & BRENT, D. H., eds. *SPSS: statistical package for the social sciences*: 468–514. New York: McGraw–Hill.
- KING, L. C. 1963. *South African scenery*. Edinburgh: Oliver & Boyd.
- KINGDON, J. 1974. *East African mammals IIA & IIB*. London & New York: Academic Press.
- KLEIN, R. G. 1972a. Preliminary report on the July through September 1970 excavations at Nelson Bay Cave, Plettenberg Bay (Cape Province, South Africa). *Palaeoecol. Afr.* **6**: 177–208.
- KLEIN, R. G. 1972b. The late Quaternary mammalian fauna of Nelson Bay Cave (Cape Province, South Africa): its implications for megafaunal extinctions and for environmental and cultural change. *Quat. Res.* **2**: 135–142.
- KLEIN, R. G. 1974a. Environment and subsistence of prehistoric man in the southern Cape Province, South Africa. *Wld Archaeol.* **5**: 249–284.
- KLEIN, R. G. 1974b. On the taxonomic status, distribution and ecology of the blue antelope, *Hippotragus leucophaeus* (Pallas, 1766). *Ann. S. Afr. Mus.* **65**: 99–143.
- KLEIN, R. G. 1975. Middle Stone Age man–animal relationships in southern Africa: evidence from Die Kelders and Klasies River Mouth. *Science* **190**: 265–267.
- KLEIN, R. G. 1976. The mammalian fauna of the Klasies River Mouth sites, southern Cape Province, South Africa. *S. Afr. archaeol. Bull.* **31**: 75–98.
- KLEIN, R. G. 1977. The ecology of early man in southern Africa. *Science* **197**: 115–126.

- KLEIN, R. G. 1978. A preliminary report on the larger mammals from the Boomplaas Stone Age site, Cango Valley, Oudtshoorn District, South Africa. *S. Afr. archaeol. Bull.* **33**: 66-75.
- KLEIN, R. G. 1979. Stone Age exploitation of animals in southern Africa. *Amer. Sci.* **67**: 151-160.
- KLEIN, R. G. 1981. Later Stone Age subsistence at Byeneskranskop Cave, South Africa. In: HARDING, R. S. O. & TELEKI, G., eds. *Omnivorous primates: gathering and hunting in human evolution*: 166-190. New York: Columbia University Press.
- KLOMP, H. 1962. The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal populations. *Arch. Néerl. Zool.* **15**: 68-109.
- KNOX, E. 1976. Upper alveolar patterns of some Muridae in Queensland and Papua New Guinea. *Mem. Queensland Mus.* **17**: 457-460.
- KOWALSKI, K. 1971. The biostratigraphy and paleoecology of Late Cenozoic mammals of Europe and Asia. In: TUREKIAN, K. K., ed. *The late Cenozoic glacial ages*: 465-477. New Haven: Yale University Press.
- KREBS, C. J. 1972. *Ecology*. New York: Harper & Row.
- KRUGER, F. J. 1977. Ecological reserves in the Cape fynbos: towards a strategy for conservation. *S. Afr. J. Sci.* **73**: 81-85.
- KRUGER, F. J. 1979. South African heathlands. In: SPECHT, R. L., ed. *Ecosystems of the world*. 9A. *Heathlands and related shrublands. Descriptive studies*: 19-80. Amsterdam: Elsevier.
- KUKLA, G. J. 1975. Loess stratigraphy of central Europe. In: BUTZER, K. W. & ISAAC, G. LL, eds. *After the australopithecines*: 99-188. The Hague & Paris: Mouton.
- KUKLA, G. J. 1977. Pleistocene land-sea correlations. 1. Europe. *Earth-Sci. Rev.* **13**: 307-374.
- LAMPREY, H. F. 1963. Ecological separation of the large mammal species in the Tarangire Game Reserve, Tanganyika. *E. Afr. Wildl. J.* **1**: 63-92.
- LIVINGSTONE, D. A. 1975. Late Quaternary climatic change in Africa. *A. Rev. Ecol. Syst.* **6**: 249-280.
- LUZ, B. 1973. Stratigraphic and paleoclimatic analysis of Late Pleistocene tropical southeast Pacific cores (with appendix by N. J. Shackleton). *Quat. Res.* **3**: 56-72.
- LUZ, B. 1977. Late Pleistocene paleoclimates of the south Pacific based on statistical analysis of planktonic foraminifers. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **22**: 61-78.
- LYNCH, C. D. 1975. The distribution of mammals in the Orange Free State, South Africa. *Navors. nas. Mus. Bloemfontein* **3**: 109-139.
- MANGERUD, J., SØNSTEGAARD, E. & SEJRUP, H.-P. 1979. Correlation of the Eemian (interglacial) Stage and the deep-sea oxygen isotope stratigraphy. *Nature, Lond.* **277**: 189-192.
- MARTIN, A. R. H. 1962. Evidence relating the Quaternary history of the Wilderness lakes. *Trans. Proc. geol. Soc. S. Afr.* **65**: 19-42.
- MARTIN, A. R. H. 1968. Pollen analysis of Groenvlei lake sediments, Knysna (South Africa). *Rev. Palaeobotan. Palynol.* **7**: 107-144.
- MARTIN, A. R. H. 1969. Final report on the palynology of Groenvlei, Knysna, South Africa. *Palaeoecol. Afr.* **4**: 190-191.
- MAZEL, A. D. & PARKINGTON, J. E. 1978. Sandy Bay revisited: variability among Late Stone Age tools. *S. Afr. J. Sci.* **74**: 381-382.
- McLACHLAN, G. R. & LIVERSIDGE, R. 1970. *Roberts birds of South Africa*. Johannesburg: Trustees of the John Voelcker Bird Book Fund.
- MEESTER, J. 1955. A mammal survey of the S.A. Lombard Nature Reserve (1954). *Fauna Flora, Pretoria* **6**: 45-57.
- MEESTER, J. 1958. Variation in the shrew genus *Myosorex* in southern Africa. *J. Mammal.* **39**: 325-339.
- MEESTER, J. 1961. A taxonomic revision of southern African *Crocridura* (Mammalia: Insectivora). *Ann. Mag. nat. Hist.* **4**: 561-571.
- MEESTER, J. 1962. The distribution of *Crocridura* Wrangler in southern Africa. *Ann. Cape prov. Mus.* **2**: 77-84.
- MEESTER, J. 1963. A systematic revision of the shrew genus *Crocridura* in southern Africa. *Transv. Mus. Mem.* **13**: 1-127.
- MEESTER, J. & SETZER, H. W., eds. 1971. *The mammals of Africa: an identification manual*. Washington: Smithsonian Institution Press.

- MISONNE, X. 1969. African and Indo-Australian Muridae: evolutionary trends. *Ann. Mus. r. Afr. cent. (in-8°) (Sci. zool.)* **172**: 1–219.
- MISONNE, X. 1971. Rodentia. In: MEESTER, J. & SETZER, H. W., eds. *The mammals of Africa: an identification manual*. Washington: Smithsonian Institution Press.
- MOFFETT, R. O. & DEACON, H. J. 1977. The flora and vegetation in the surrounds of Boomplaas Cave, Cango Valley. *S. Afr. archaeol. Bull.* **32**: 127–145.
- MONTAGGIONI, L. 1976. Holocene submergence on Réunion Island (Indian Ocean). In: *Proc. 5th Afr. Soc. Quat. Res., Ann. S. Afr. Mus.* **71**: 69–75.
- MÖRNER, N.-A. 1978. Palaeogeoidal changes and palaeoecological changes in Africa with respect to real and apparent palaeoclimatic changes. *Palaeoecol. Afr.* **10**: 1–12.
- NEAL, B. R. 1970. The habitat distribution and activity of a rodent population in western Uganda, with particular reference to the effects of burning. *Rev. Zool. Bot. afr.* **81**: 29–50.
- NEAL, B. R. & COCK, A. G. 1969. An analysis of the selection of small African mammals by two break-back traps. *J. Zool.* **158**: 335–340.
- NEL, J. A. J. & PRETORIUS, J. J. L. 1971. A note on the smaller mammals of the Mountain Zebra National Park. *Koedoe* **14**: 99–110.
- NEL, J. A. J. & RAUTENBACH, I. L. 1975. Habitat use and community structure of rodents in the southern Kalahari. *Mammalia* **39**: 9–29.
- NIE, N. H., HULL, C. H., JENKINS, J. G., STEINBRENNER, K. & BENT, D. H. 1975. *SPSS: statistical package for the social sciences*. New York: McGraw-Hill.
- ODUM, E. P. 1971. *Fundamentals of ecology*. Philadelphia: W. B. Saunders.
- PARKINGTON, J. E. 1972. Seasonal mobility in the Later Stone Age. *Afr. Stud.* **31**: 223–243.
- PARKINGTON, J. E. 1976. Coastal settlement between the mouths of the Berg and Olifants Rivers, Cape Province. *S. Afr. archaeol. Bull.* **31**: 127–140.
- PATERSON, W. S. B., KOERNER, R. M., FISHER, D., JOHNSEN, S. J., CLAUSEN, H. B., DANSGAARD, W., BUCHER, P. & OESCHGER, H. 1977. An oxygen isotope climatic record from the Devon Island ice cap, Arctic Canada. *Nature, Lond.* **266**: 508–511.
- PIENAAR, U. DE V. 1964. The small mammals of the Kruger National Park: a systematic list and zoogeography. *Koedoe* **7**: 1–25.
- RAUTENBACH, I. L. 1971. Notes on the small mammals of the Kalahari Gemsbok National Park. *Koedoe* **14**: 137–144.
- RAUTENBACH, I. L. 1976. A survey of the mammals occurring in the Golden Gate Highlands National Park. *Koedoe* **19**: 133–144.
- RAUTENBACH, I. L. & NEL, J. A. J. 1975. Further records of smaller mammals of the Kalahari Gemsbok National Park. *Koedoe* **18**: 195–198.
- ROBERTS, A. 1951. *The mammals of South Africa*. Johannesburg: Trustees of 'The mammals of South Africa' Book Fund.
- ROSENZWEIG, M. L. & WINAKUR, J. 1969. Population ecology of desert communities: habitats and environmental complexity. *Ecology* **50**: 558–572.
- ROSEVEAR, D. R. 1969. *The rodents of West Africa*. London: Trustees of the British Museum (Natural History).
- ROUSSOUW, P. J., MEYER, E. I., MULDER, M. P. & STOCKEN, C. G. 1964. *Die geologie van die Swartberge, die Kangovallei en die omgewing van Prins Albert, K.P.* Pretoria: Dept. of Mines, Geological Survey.
- RUMMEL, R. J. 1967. Understanding factor analysis. *J. Conflict Resolution* **11**: 444–480.
- SAINT GIRONS, M.-C. 1977. Morphologie végétale et répartition des Mammifères. *Bijdr. Dierk.* **47**: 120–130.
- SAMPSON, C. G. 1974. *The Stone Age archaeology of southern Africa*. New York & London: Academic Press.
- SANCETTA, C., IMBRIE, J. & KIPP, N. G. 1973. Climatic record of the past 130 000 years in north Atlantic deep-sea core V23–82: correlation with the terrestrial record. *Quat. Res.* **3**: 110–116.
- SCHALKE, H. J. W. G. 1973. The Upper Quaternary of the Cape Flats area (Cape Province, South Africa) *Scripta geol.* **15**: 1–57.
- SCHAPER, I. 1930. *The Khoisan peoples of South Africa. Bushmen and Hottentots*. London: George Routledge & Sons.
- SCHRIRE, C. 1962. Oakhurst: a re-examination and vindication. *S. Afr. archaeol. Bull.* **17**: 181–195.

- SCHULZ, K. H. 1953. The control of veld rodents responsible for damage to pine forests in the eastern Transvaal. *Public Health (Johannesburg)* **17**: 402-465.
- SCHULZE, B. R. 1965. *Climate of South Africa. Part 8: general survey*. Pretoria: Government Printer.
- SCHWEITZER, F. R. 1970. A preliminary report of excavations at a cave at Die Kelders. *S. Afr. archaeol. Bull* **25**: 136-138.
- SCHWEITZER, F. R. & SCOTT, K. 1973. Early occurrence of domestic sheep in sub-Saharan Africa. *Nature, Lond.* **241**: 547.
- SCHWEITZER, F. R. & WILSON, M. L. 1978. A preliminary report on excavations at Byneskranskop, Bredasdorp District, Cape. *S. Afr. archaeol. Bull.* **33**: 134-140.
- SCLATER, W. L. 1900-1. *The mammals of South Africa*. London: R. H. Porter.
- SCOTT, L. & VOGEL, J. C. 1978. Pollen analysis of the thermal spring deposit at Wonderkrater (Transvaal, South Africa). *Palaeoecol. Afr.* **10**: 155-162.
- SERVICE, E. R. 1966. *The hunters*. Englewood Cliffs: Prentice-Hall.
- SHACKLETON, N. J. 1973. Oxygen isotope analysis as a means of determining season of occupation of prehistoric midden sites. *Archaeometry* **15**: 133-141.
- SHACKLETON, N. J. 1975. The stratigraphic record of deep-sea cores and its implications for the assessment of glacials, interglacials, stadials and interstadials in the mid-Pleistocene. In: BUTZER, K. W. & ISAAC, G. LL., eds. *After the australopithecines*: 1-24. The Hague & Paris: Mouton.
- SHACKLETON, N. J. & MATTHEWS, R. K. 1977. Oxygen isotope stratigraphy of late Pleistocene coral terraces in Barbados. *Nature, Lond.* **268**: 618-620.
- SHACKLETON, N. J. & OPDYKE, N. D. 1973. Oxygen isotope and paleomagnetic stratigraphy of equatorial core V28-238: oxygen isotope temperatures and ice volumes on a 10^3 and 10^6 scale. *Quat. Res.* **3**: 39-55.
- SHACKLETON, N. J. & OPDYKE, N. D. 1976. Oxygen-isotope and paleomagnetic stratigraphy of Pacific core V28-239 late Pliocene to latest Pleistocene. In: CLINE, R. M. & HAYS, J. D., eds. *Investigation of late Quaternary paleoceanography and paleoclimatology*. *Geol. Soc. Amer. Mem.* **145**: 449-464.
- SHEPPE, W. A. 1973. Notes on Zambian rodents and shrews. *Puku* **7**: 167-190.
- SHEPPE, W. A. & OSBORNE, T. 1971. Patterns of use of a flood plain by Zambian mammals. *Ecol. monogr.* **41**: 179-205.
- SHORTRIDGE, G. C. 1934. *The mammals of South West Africa*. London: William Heinemann.
- SHORTRIDGE, G. C. 1942. Field notes on the first and second expeditions of the Cape museums' mammal survey of the Cape Province: descriptions of some new subgenera and subspecies. *Ann. S. Afr. Mus.* **36**: 27-100.
- SIMPSON, G. G., ROE, A. & LEWONTIN, R. C. 1960. *Quantitative zoology*. New York: Harcourt Brace.
- SMITHERS, R. H. N. 1971. The mammals of Botswana. *Natl Mus. Rhodesia Mem.* **4**: 1-340.
- SMUTS, J. 1832. *Dissertatio zoologica, enumerationem mammalium capensium*. Leiden: J. C. Cyfveer.
- SOUTHERN, H. N. 1954. Tawny owls and their prey. *Ibis* **96**: 348-410.
- SPARKS, J. & SOPER, T. 1972. *Owls. Their natural and unnatural history*. Newton Abbot: David & Charles.
- STEYN, P. & TREDGOLD, D. 1977. Observations on the Cape eagle owl. *Bokmakierie* **29**: 31-42.
- STUART, C. T. 1976. Diet of the black backed jackal *Canis mesomelas* in the Namib Desert, South West Africa. *Zool. afr.* **11**: 193-205.
- STUART, C. T. 1977. Analysis of *Felis libyca* and *Genetta genetta* scats from the central Namib Desert, South West Africa. *Zool. afr.* **12**: 239-241.
- STUART, C. T. n.d. Preliminary report on a rodent and insectivore survey in the Jonkershoek Valley, Stellenbosch. Unpublished report, Cape Provincial Administration.
- SWANEPOEL, P. 1975. Small mammals of the Addo Elephant National Park. *Koedoe* **18**: 103-137.
- SYCH, L. 1965. Fossil Leporidae from the Pliocene and Pleistocene of Poland. *Acta zool. Cracov.* **10**: 1.
- TALMA, A. S., VOGEL, J. C. & PARTIDGE, T. C. 1974. Isotopic contents of some Transvaal speleothems and their palaeoclimatic significance. *S. Afr. J. Sci.* **70**: 135-140.
- TANKARD, A. J. 1976a. The stratigraphy of a coastal cave and its palaeoclimatic significance. *Palaeoecol. Afr.* **9**: 151-159.

- TANKARD, A. J. 1976b. Cenozoic sea-level changes: a discussion. In: *Proc. sth Afr. Soc. Quat. Res., Ann S. Afr. Mus.* **71**: 1–17.
- TANKARD, A. J. & SCHWEITZER, F. R. 1974. The geology of Die Kelders Cave and environs: a palaeoenvironmental study. *S. Afr. J. Sci.* **70**: 365–369.
- TANKARD, A. J. & SCHWEITZER, F. R. 1976. Textural analysis of cave sediments: Die Kelders, Cape Province, South Africa. In: DAVIDSON, D. A. & SHACKLEY, M. L., eds. *Geoarchoeology*: 289–316. London: Duckworth.
- TAYLOR, H. C. 1961. Ecological account of a remnant of coastal forest near Stanford, Cape Province. *J. S. Afr. Bot.* **27**: 153–165.
- TAYLOR, H. C. 1978. Capensis. In: WERGER, M. J. A., ed. *Biogeography and ecology of southern Africa. Monogr. Biol.* **31**: 171–229.
- TCHERNOV, E. 1968. *Succession of rodent faunas during the Upper Pleistocene of Israel. Mammalia depicta*. Hamburg: Verlag Paul Parey.
- TCHERNOV, E. 1975. Rodent faunas and environmental change in the Pleistocene of Israel. In: PRAKASH, I. & GHOSH, P. K., eds. *Rodents in desert environments*: 331–362. The Hague: W. Junk.
- THOMAS, O. & SCHWANN, H. 1904. The Rudd exploration of South Africa. I—British Namaqualand. *Proc. zool. Soc. Lond.* 1904: 171–183.
- THOMAS, O. & SCHWANN, H. 1905a. The Rudd exploration of South Africa. II—Wakkerstroom, S.E. Transvaal. *Proc. zool. Soc. Lond.* 1905: 129–138.
- THOMAS, O. & SCHWANN, H. 1905b. The Rudd exploration of South Africa. III—Zululand. *Proc. zool. Soc. Lond.* 1905: 254–276.
- THOMAS, O. & SCHWANN, H. 1906a. The Rudd exploration of South Africa. IV—Knysna. *Proc. zool. Soc. Lond.* 1906: 159–168.
- THOMAS, O. & SCHWANN, H. 1906b. The Rudd exploration of South Africa. V—N.E. Transvaal. *Proc. zool. Soc. Lond.* 1906: 575–591.
- TRIGGER, B. G. 1971. Archaeology and ecology. *Wld Archaeol.* **2**: 321–336.
- TRUSWELL, J. F. 1971. *The geological evolution of South Africa*. Cape Town: Purnell.
- VAN DER HAMMEN, T., WUJSTRA, T. A. & ZAGWIJN, W. H. 1971. The floral record of the late Cenozoic of Europe. In: TUREKIAN, K. K., ed. *The late Cenozoic glacial ages*: 390–424. New Haven: Yale University Press.
- VAN ZINDEREN BAKKER, E. M. 1957. A pollen analytical investigation of the Florisbad deposits (South Africa). In: CLARK, J. D., ed. *Third Pan-African Congress on Prehistory, Livingstone 1955*: 56–67. London: Chatto & Windus.
- VAN ZINDEREN BAKKER, E. M. 1976. The evolution of Late-Quaternary palaeoclimates of southern Africa. *Palaeoecol. Afr.* **9**: 160–202.
- VAN ZINDEREN BAKKER, E. M. & BUTZER, K. W. 1973. Quaternary environmental changes in southern Africa. *Soil Sci.* **116**: 236–248.
- VERNON, C. J. 1972. An analysis of owl pellets collected in southern Africa. *Ostrich* **43**: 109–124.
- VESEY-FITZGERALD, D. F. 1964. Mammals of the Rukwa Valley. *Tanganyika Notes & Records* **62**: 61–72.
- VESEY-FITZGERALD, D. F. 1966. The habits and habitats of small rodents in the Congo River catchment region of Zambia and Tanzania. *Zool. afr.* **2**: 111–122.
- VINCENT, E. 1972. Climatic change at the Pleistocene–Holocene boundary in the southwestern Indian Ocean. *Palaeoecol. Afr.* **6**: 45–54.
- WELLINGTON, J. H. 1955. *Southern Africa—a geographical study. I. Physical geography*. Cambridge: Cambridge University Press.
- WERGER, M. J. A. 1978. The Karoo–Namib Region. In: WERGER, M. J. A., ed. *Biogeography and ecology of southern Africa. Monogr. Biol.* **31**: 231–299.
- WHITE, F. 1978. The Afromontane Region. In: WERGER, M. J. A., ed. *Biogeography and ecology of southern Africa. Monogr. Biol.* **31**: 463–513.
- WINGATE, L. R. & MEESTER, J. 1977. A field test of six types of live-trap for African rodents. *Zool. afr.* **12**: 215–223.
- WOILLARD, G. M. 1978a. Grande Pile peat bog: a continuous pollen record for the last 140 000 years. *Quat. Res.* **9**: 1–21.
- WOILLARD, G. M. 1978b. Végétation et climat des derniers 140 000 ans dans la tourbière de la Grande Pile (N.E. France). *Palaeoecol. afr.* **10**: 125–134.

- WYMER, J. J. & SINGER, R. 1972. Middle Stone Age occupational settlements on the Tsitsikama coast, eastern Cape Province, South Africa. *In*: UCKO, P. J., TRINGHAM, R. & DIMBLEBY, G. W., eds. *Man, settlement and urbanism*: 207–210. London: Duckworth.
- YELLEN, J. E. 1977. Long-term hunter-gatherer adaptation to desert environments: a biogeographical perspective. *Wld Archaeol.* **8**: 262–274.
- YELLEN, J. E. & LEE, R. B. 1976. The Dobe-/Du/da environment. *In*: LEE, R. B., & DE VORE, I., eds. *Kalahari hunter-gatherers*: 27–46. Cambridge & London: Harvard University Press.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM–A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

(a) The Figures, Maps and Tables of the paper when referred to in the text

e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'

(b) The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names

e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene

(c) Scientific names, but not their vernacular derivatives

e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

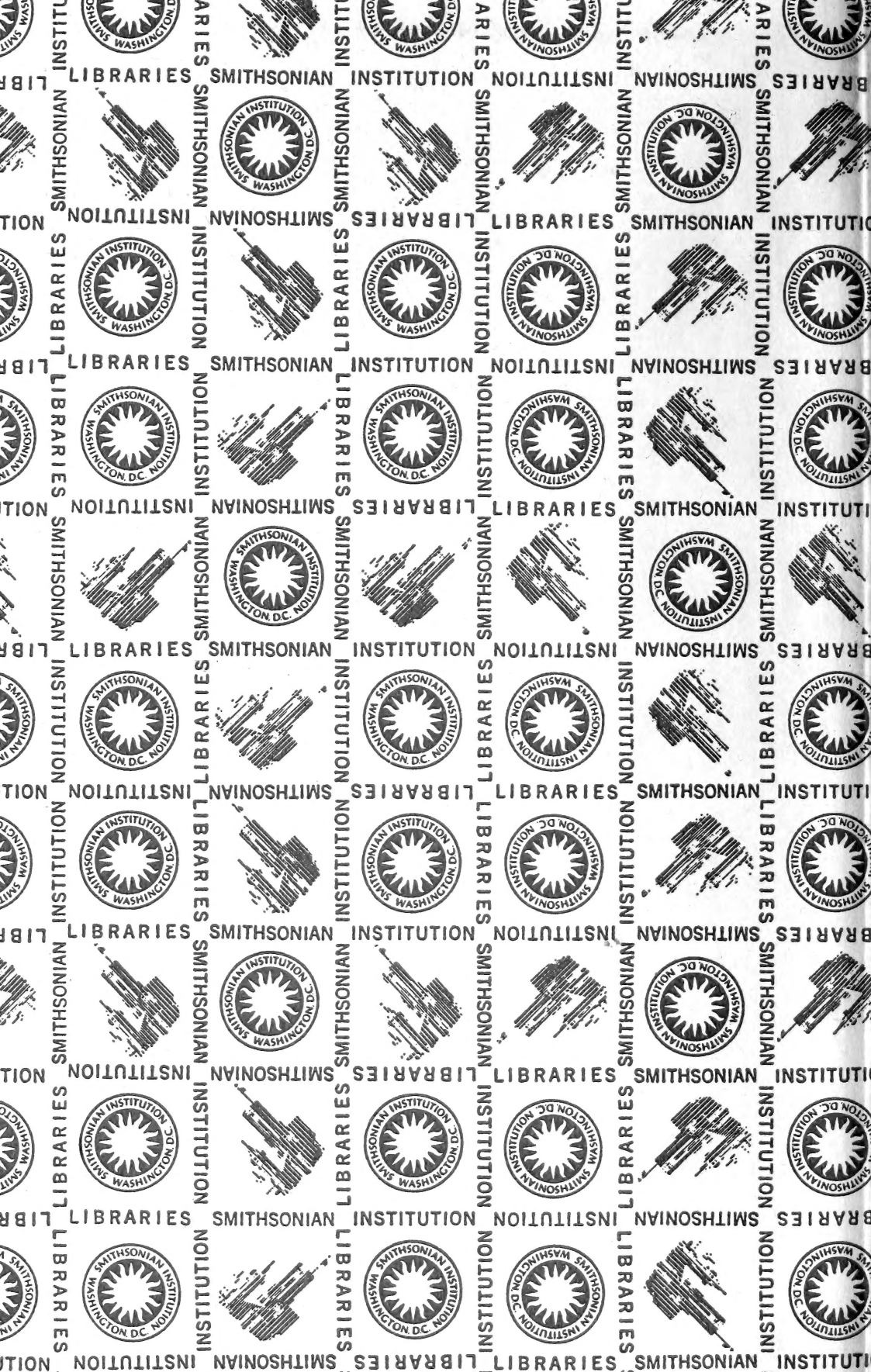
Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

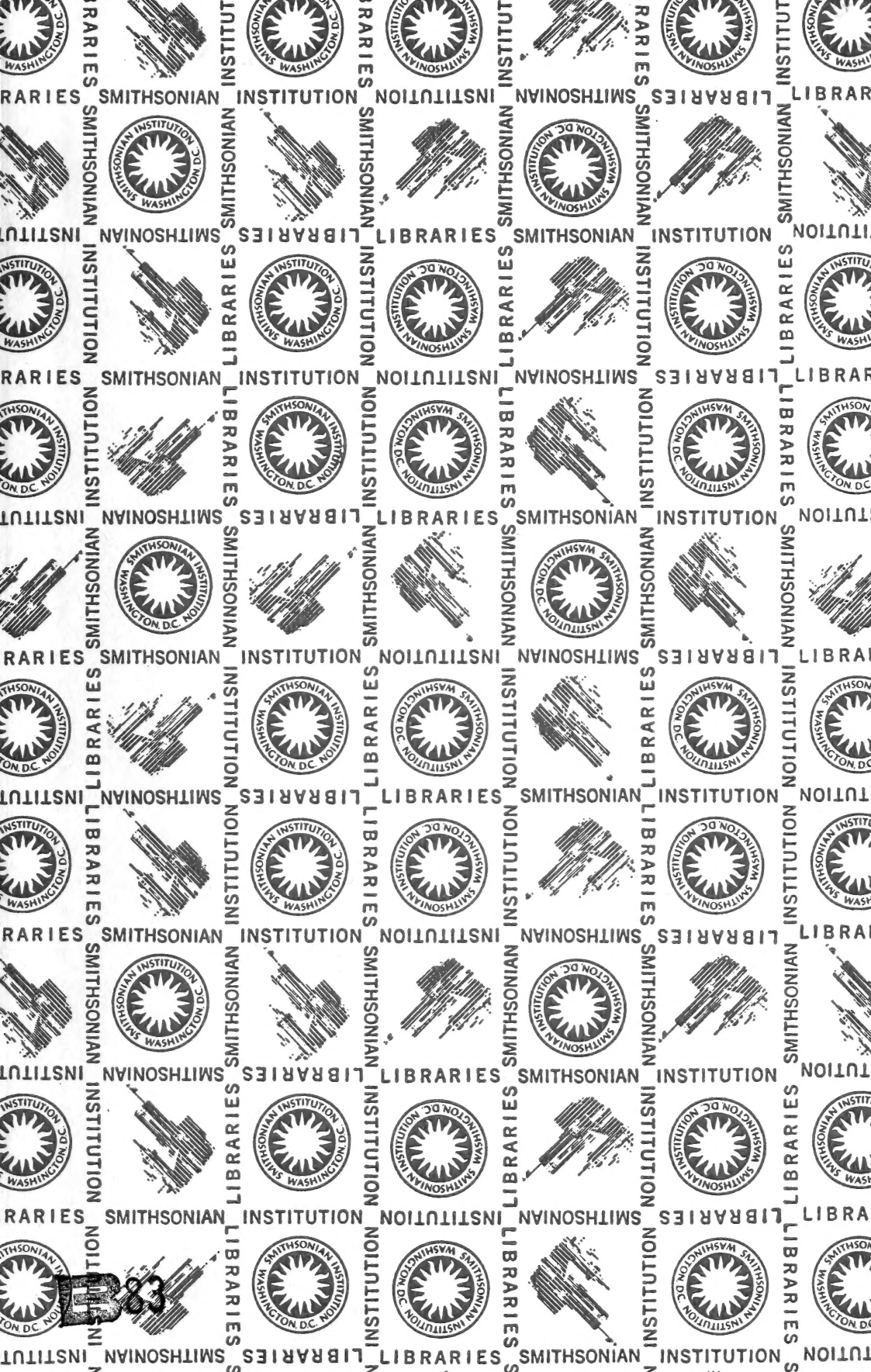
Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

D. M. AVERY

MICROMAMMALS AS
PALAEOENVIRONMENTAL INDICATORS AND
AN INTERPRETATION OF THE LATE
QUATERNARY IN THE SOUTHERN CAPE
PROVINCE, SOUTH AFRICA







83

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 01206 6775